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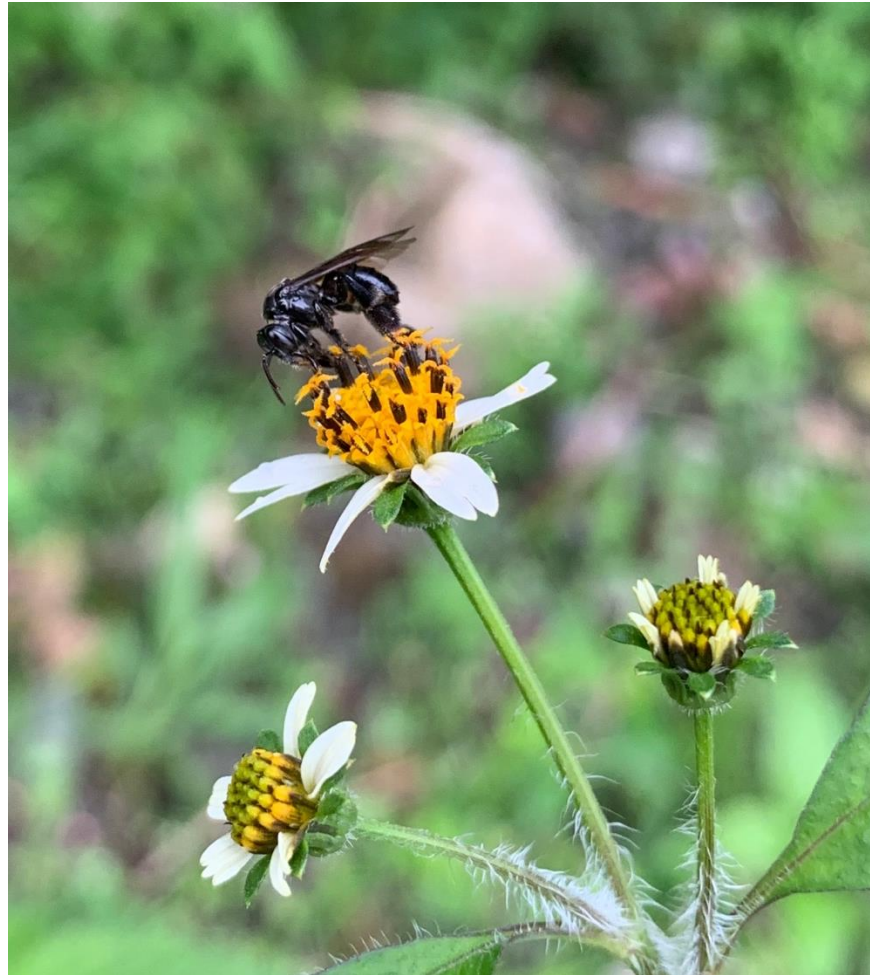Part of the Biodiversity Commons, Botany Commons, Entomology Commons, Environmental Monitoring Commons, and the Plant Biology Commons

Community complexity of a pollination network:
Analysis of plant-pollinator interactions in the eastern Ecuadorian cloud forest

Apidae species pollinating flower of *Bidens* species close to the Río Zuñac reserve in the eastern Ecuadorian cloud forest. Photo by author.

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Abstract

Global declines in pollinators and temporal/spatial mismatches between plants and pollinators threaten the integrity of plant-pollinator networks. Ecological network analysis provides a powerful framework for understanding the dynamics of plant-pollinator networks and measures of community complexity that can help inform areas of priority in conservation. This study observed a plant-pollinator network in a secondary forest close to the Río Zuñac Reserve in the eastern Ecuadorian cloud forest to identify assemblages of plants and pollinators and evaluate measures of community complexity, including specialization and nestedness. Flowering plants were identified and observed along a 1.2 km transect, and floral visitors to these plants were identified to morphospecies. The network was observed for a total of 26.5 hours. High species richness of plants and potential pollinators were observed in the network, with low frequencies of interactions between mutualist partners. The network had a high value of network-level specialization and a low degree of nestedness, which imply that the network does not have the ability to robustly respond to perturbations. Animals tended to be more specialized than plants, highlighting the importance of floral diversity in maintaining animal pollinators. Of the most abundant animal taxa observed, the family Apidae had the highest level of generalization, marking it as an important group of pollinators at the network level. This study presents a baseline understanding of pollination networks in the Río Zuñac reserve and concludes that network interactions are relatively specialized. Understanding pollination networks, especially in under-studied Neotropical environments like the cloud forest, represent an important first step in creating ecosystem-level conservation priorities and supporting robustness in ecological networks.

Keywords: pollination, ecological networks, mutualistic networks, specialization, cloud forest, Río Zuñac

Resumen

Caídas globales de polinizadores y desajustes espaciales o temporales entre plantas y polinizadores amenazan la integridad de las redes de polinización. El análisis de redes ecológicas provee un marco potente para entender las dinámicas de redes de polinización y las medidas de complejidad de las comunidades para informar áreas de prioridad en la conservación. Este estudio fue basado en la observación de una red de polinización en un bosque secundario cerca de la reserva Río Zuñac en el bosque nublado oriental del Ecuador para identificar ensamblajes de plantas y polinizadores y evaluar medidas de complejidad de la comunidad, incluyendo especialización y anidamiento. Las plantas con flores fueron identificadas y observadas a lo largo de un transecto de 1.2 km, y visitantes florales a estas plantas fueron identificados a nivel de morfoespecie. La red fue observada por un total de 26.5 horas. Se observó una alta riqueza de especies de plantas y polinizadores potenciales con frecuencias bajas de interacciones entre compañeros mutualistas. Había un valor alto de especialización al nivel de la red y un nivel bajo de anidamiento, lo cual indica que esta red no tiene la habilidad de responder robustamente a perturbaciones. Los animales tendieron a ser más especializados que plantas, destacando la importancia de una diversidad florística en el mantenimiento de polinizadores. De los taxones más abundantes de animales, la familia Apidae tuvo el nivel más alto de generalización, marcando la familia como un grupo importante de polinizadores a nivel de la red. Este estudio presenta un punto de referencia de las dinámicas de redes de polinización en la reserva Río Zuñac y concluye que las interacciones de la red son relativamente especializadas. Entender redes de polinización, especialmente en ambientes Neotropicales pocos estudiados como los

bosques nublados, representa un importante primer paso para crear prioridades de conservación al nivel del ecosistema y apoyar la robustez en redes ecológicas.

Palabras claves: polinización, redes ecológicas, redes mutualistas, especialización, bosque nublado, Río Zuñac

Acknowledgements

Agradecimientos

Introduction

Animal pollination is a key service in maintaining the functional integrity of ecosystems. Animals pollinate 87.5% of angiosperms, and this number increases to 94% in tropical communities (Ollerton *et al.,* 2011). These interactions ensure the reproductive success of plants and the survival of a diverse set of animal pollinators. However, global declines in pollinators, driven by factors such as land-use change and climate change (Potts *et al.,* 2010), impair the vitality of this interaction, which may have cascading effects that threaten the food base of many species (Kearns & Inouye, 1997). Pollination interactions may not happen at the right time or in the right place because of ongoing changes in the distribution and phenology of plants and pollinators caused by climate change (Hickling et al., 2006; Flores et al., 2023; Parmesan, 2007). Modeling of future climate change scenarios in the Neotropics predicts habitat reduction of plants and pollinators and consequent mismatches (Bezerra *et al.,* 2019). Therefore, understanding the inter-species dynamics of pollination represents a crucial first step to addressing the negative impacts of anthropogenic disturbances to ensure the survival of plants and their pollinators.

While studies of specific pollination interactions provide fine-scale insights into the roles of certain species (Koptur & Khorsand, 2018), considerations of pollination interactions on a community level enables analysis of ecosystem robustness and provides baseline knowledge of ecosystem-wide dynamics to inform further studies (Kaiser-Bunbury *et al.,* 2017; Memmott 1999). Ecological network analysis has emerged as a powerful tool to understand the interactions between plants and pollinators as an interconnected entity (Trøjelsgaard & Olesen, 2013). Using

bipartite sets consisting of flowering plants and their animal pollinators, pollination network analysis uses different measures of community complexity that reveal how ecosystems work. These measures of community complexity can then be used to compare networks across time and space to understand the factors that lead to variations in the composition of plant-pollinator assemblages and how they specialize or generalize (Cuartas-Hernández & Medel, 2015; Olesen & Jordano, 2002).

The latitudinal diversity gradient describes the widely observed phenomena of increasing biodiversity, including insect and plant diversity, with increasing proximity to the tropics (Hillebrand, 2004). In mutualistic networks, specialization is understood as ecological niche breadth. The effects of this increased diversity on the specificity of mutualistic interactions remains contested, with some studies concluding that increasing diversity leads to increased specificity in insect-plant interactions (Dyer *et al.,* 2007) and some rejecting the hypothesis of greater specialization (Novotny *et al.,* 2006). When considering the networks of mutualistic interactions between animals and plants (e.g., pollination and seed dispersal), Schleuning *et al.* (2012) found that specialization decreased in the tropics, suggesting that specialization is a response to low plant diversity. Olesen and Jordano (2002) found that the generalization of plants, not animals, in pollination networks decreased marginally towards the tropics, but these patterns vary within taxonomic groups. Given the conflicting findings of various studies and reviews, further investigation into trends of generalization in pollination networks in specific areas of the Neotropics will yield additional understandings of these ecological interactions.

The question of specialized or generalized interactions among pollination networks is important to consider given ongoing disruptions to pollination ecology. Pollination networks are characterized by generalized interactions, with few highly specialized interactions within networks (Jordano 1987). Generalized networks are more tolerant to species extinctions, although the extinction of highly connected species may still provoke a collapse of the network (Kaiser-Bunbury *et al.,* 2010). With the threats of anthropogenic disturbances and climate change, species may become locally extinct and/or phenologically mismatched but generalized networks may compensate for these disturbances because of redundancy in their interactions. Using ecological networks as a framework to understand pollination ecology provides insights into the robustness of the network by evaluating patterns of generalization and identifying the most highly connected species.

Montane cloud forests are tropical ecosystems characterized by persistent ground-level cloud (Grubb, 1977). Andean cloud forests are recognized as a global biodiversity hotspot (Myers *et al.,* 2000) and contain extremely high levels of endemism (Foster, 2001). Few studies have examined pollination ecology in the Andean cloud forests using ecological networks (but see Cuartas-Hernández & Medel, 2015). Given the high altitudinal gradient and biodiversity, the study of cloud forest pollination interactions using ecological network analysis contributes important insights into the role of abiotic factors in the complexity of pollination networks (Cuartas-Hernández & Medel, 2015). This study aims to use ecological network analysis to evaluate measures of community complexity in a pollination network in the eastern Ecuadorian cloud forest. High generalization and nestedness lead to redundancy in mutualistic interactions which lead to robustness in pollination networks (Memmott *et al.,* 2004). Special consideration will be given to these metrics. Therefore, this study will compare assemblages of species interactions and measures of indices of network topology to answer the following questions: (1) Which assemblages of flowering plants and insect pollinators interact with each other? and (2) How generalized are the interactions between plants and animal pollinators at both network and

taxa level? To answer these questions, this study examined the pollination network in a secondary forest outside the Río Zuñac reserve in the Tungurahua province of eastern Ecuador. Data was taken on all plant and potential pollinator interactions along a 1.2 km transect to construct an interaction matrix of the pollination network during a given period. The network metrics of the matrix were analyzed to understand the assemblages of mutualist partners and the ways they specialize.

This study aims to contribute to the baseline literature on the pollination ecology of the Ecuadorian cloud forest by documenting the interactions between taxonomic groups of plants and insect pollinators. This study also aims to understand the robustness of pollination networks using quantifications of specialization in plant and insect pollinator species. Given anthropogenic climate change and land-use change, cloud forest ecosystems will continue to face threats to biodiversity and ecosystem functions (Hermes *et al.,* 2018). By analyzing the degrees of specialist interactions in pollination networks, we can further understand the robustness of networks to disturbances and their tolerance to potential extinctions.
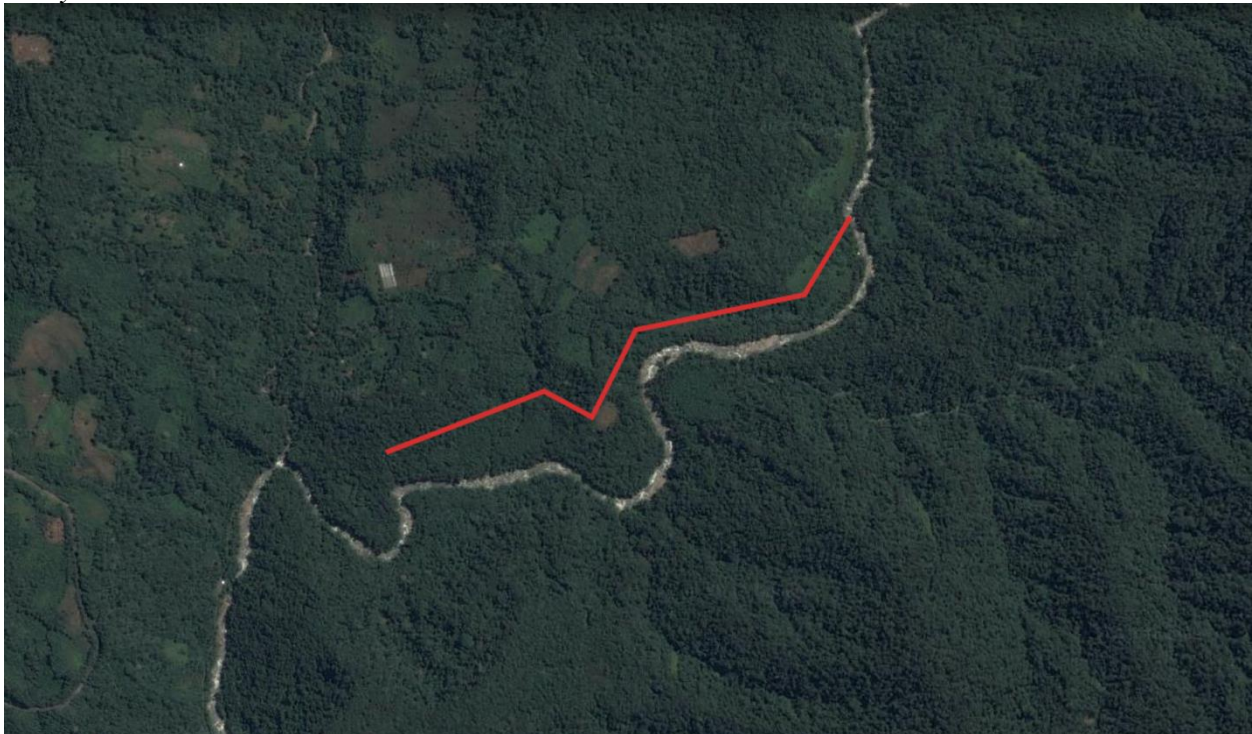
Materials and Methods
Study site

Figure 1. Transect along trail leading to Río Zuñac reserve. Courtesy Google Earth.
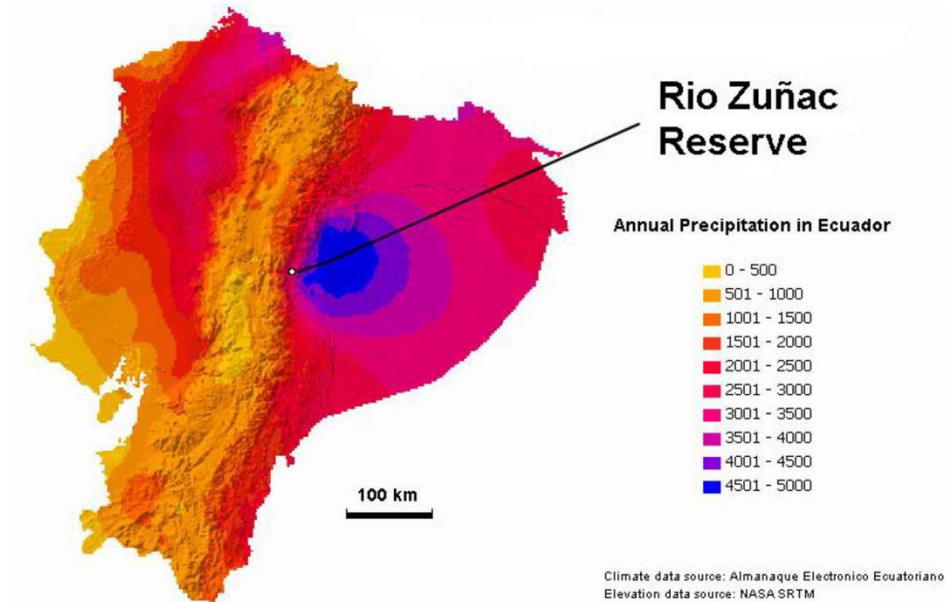
Figure 2. Precipitation map of Ecuador in mm per year, with Río Zuñac reserve indicated with white dot (Kullberg, 2017).

Observations were conducted from November 14 to December 1, 2023, on the trail leading to the Río Zuñac reserve (Figure 1). A 1.2 km transect was set up along the trail, with markers every 20-30 m. The EcoMinga Foundation oversees the reserve, which is in the Baños Canton of Tungurahua province. The trail is in mature secondary forest next to land used for agriculture. The reserve is in the eastern Ecuadorian cloud forest and receives high amounts of rain (Figure 2). The average rainfall during November, when this study was conducted, is 269mm, and the yearly average was 2665mm (Climate Data). The temperature remains relatively constant throughout the year, with an average of 16.3 °C. Observations took place at an elevation between 1300 and 1400m.

Materials

To identify and set up the transect, a measuring tape, flagging tape, and the Gaia mobile app were used. A butterfly net, aspirator, pincers, plastic vials with an 80% alcohol solution, binoculars, and a mobile phone camera were used to collect or document plants and animal pollinators. A 250X digital USB microscope and petri dishes were used to identify insect pollinators, excluding Lepidoptera species that were photographed in the field.

Methodology

Observation of floral visitation

Flowering plants along the transect were photographed and later identified (Figure 3). Only plants that had visible flowers reachable with a 1-meter butterfly net were included for observations. Generally, these plants had flowers that were less than 2 meters from the ground and adjacent to the trail. Observations took place during sunny to cloudy weather between the hours of 0800 to 1800. Observations did not take place during the same hours every day because of the variable weather. Rainy weather was avoided because it reduces pollinator activity (citation). Although cloudy weather also decreases pollinator activity, it was not possible to only sample during sunny weather due to the limited hours of direct sunlight. Therefore, observations were conducted in the mornings or afternoons when it was not actively raining. Observations stopped if it began to rain.

Figure 3. Select flowering plants observed in transect. From left to right, *Burmeistera sp, Drymonia hoppii, Besleria cosmosa, Podandrogyne brachycarpa.*

Sampling efforts were concentrated on observing a representative sample of flowering plants and collecting one hour of observation time per species. A total of 39 species of flowering plants were observed. Due to consistent rainy weather and the limited period of flowering for some species, it was not possible to conduct one hour of observation per plant species. For example, some species were only found once in the transect or abscised all flowers after a few days. The observation time ranged from 5 to 220 minutes, with an average of 41 minutes per species. The system was observed for a total of 26.5 hours.

Individual periods of observation ranged between 5-15 minutes, not including handling time. Most observations were conducted while standing 1 meter away from the plant. For small herbs with minute flowers, observations were conducted at a distance closer than 1 m to see potential floral visitors. All floral visitors were documented. Animals that visited a flower for more than three seconds were considered floral visitors.

Animal floral visitors were observed and identified in different ways depending on their morphology. Hummingbirds were observed with binoculars. Lepidoptera were caught with a butterfly net and then handled to take pictures. Small flies and beetles were collected using an entomological aspirator or were picked up directly from the flower with tweezers. All other insects were collected using the butterfly net. As the insect began to fly away after visiting the flowers of the plant, it was captured using the butterfly net. Insects collected in the net or tube were transferred using tweezers to plastic tubes with an 80% ethanol solution for later identification (Hammer *et al.,* 2015). Some insects went unidentified because they were not able to be caught; some flew away before being collected in the net or aspirator, and some flew away during the transfer from the net or aspirator to the plastic tubes. Animal floral visitors were documented along with the plant species they visited and a brief morphological description to aid with future identification.

Identification of plants and animal floral visitors

Photographs of plant species were used for identification. Plants were identified to the lowest taxonomic level, either tribe, genus, or species, using similar observations in the area on the iNaturalist website and two published guides of flowering plants in the eastern cloud forest (MAE and FAO, 2015; Brito *et al.,* 2015). Almost all photos of plant species were uploaded to iNaturalist. Using the suggestions generated by the website's automated species identification tool, plants were compared to similar taxa in the area until a confident identification could be made. Most plant species were identified at least to genus level. Lepidoptera visitors were identified in the same way, and all were identified at least to genus level. Hummingbirds were

identified using eBird to find species are likely to be found in the area. All hummingbirds were identified to species level. Insects were placed in a petri dish and observed using a digital microscope. Using a dichotomous key, Triplehorn and Johnson (2005), insects were identified to family and assigned a morphospecies. Most insects were identified at the family level. Select photos of insects in the Hymenoptera and Diptera orders were uploaded to iNaturalist and identified to a lower taxonomic level with the help of iNaturalist community members. All unique morphospecies were photographed for later reference.

Although all floral visitors were documented, the analyses only include potential pollinators. A floral visitor was also considered a potential pollinator if it belonged to a taxonomic group widely regarded as important pollinators, namely bees (clade Anthophila), hoverflies (family Spechidae), and butterflies (Lepidoptera). Floral visitors were also considered potential pollinators if they visited multiple flowers for more than three seconds. Small species of flies and beetles found inside or on the reproductive structures of the flowers were also considered pollinators if they tried to fly away when disturbed, as it was assumed that they used the flowers to reproduce and later moved away to other flowers, pollinating in the process. Only two floral visitors were not considered potential pollinators. These belonged to the order Hemiptera, members of which eat plant matter and do not pollinate (Triplehorn & Johnson, 2005).

Data analysis

All analyses were run in R version 4.3.1 (R Core Team, 2019).

Network analyses

Two network matrices were constructed representing the interactions between i plant species and j floral visiting animals (Appendix A). One matrix considered interactions with floral visiting animal morphospecies. Another matrix was constructed with floral visiting animal taxa. Morphospecies were grouped by family or order. As taxa widely recognized as important pollinators, bees (order Hymenoptera, clade Anthophila), hoverflies (order Diptera, family Sphecidae), and hummingbirds (order Apodiformes, family Trochilidae) were grouped as families. All other species were grouped into orders. The orders Hymenoptera and Diptera as considered in the matrix do not include bees or hoverflies, respectively.

The matrices consist of quantitative data, meaning the number of observed interactions. Using quantitative data instead of binary presence/absence data allows for the evaluation of the strength of interactions between taxonomic groups of mutualists. From the species-level matrix, various indices were calculated to describe the network, including network size, connectance, H_2, quantitative linkage density, NODF, and interaction strength asymmetry. Indices were chosen based on their descriptive power of network structure and/or their prevalence in studies of pollination networks to enable comparisons to other networks. These indices were calculated using the 'networklevel' function of the bipartite package (Dormann *et al.,* 2008).

Network size M represents the maximum number of possible interactions in the matrix (Olesen and Jordano, 2002). M is given as

$$M = i \times j$$

Interaction I represents the total number of interactions in the network as found by the number of non-zero elements in a matrix. Connectance C gives the proportion of realized interactions I divided by the number of possible interactions M (Dunne *et al.,* 2002). C is given as

$$C = I/M$$

Two-dimensional Shannon entropy, H_2, is a quantitative measure of specialization in the network. H_2 measures network-level specialization using frequency-based (quantitative) data instead of binary (qualitative) data as is used for connectance (Blüthgen et $al.$, 2006). Interaction frequency thus is a surrogate for interaction strength. Let p_{ij} equal the proportion of interactions between a plant i species and an animal pollinator j species compared to the total number of interactions. This proportion is a qualitative measure, as opposed to the binary data of connectance. Given r rows of plant species, c columns of animal species, H_2 is given as

$$H_2 = -\sum_{P=1}^{r} \sum_{A=1}^{c} (p_{ij} \times \ln(p_{ij}))$$

The standardized index H_2' ranges from 0, representing extreme generalization, to 0, representing extreme specialization. Unlike indices based on binary data which are more dependent on sampling effort and network size, H_2' is not affected by these factors (Blüthgen et $al.$, 2006).

NODF is a measure of nestedness. Networks that have specialist species that interact with a proper subset of species that interact with more generalist species are described as highly nested (Bascompte et $al.$, 2003). NODF is based on paired overlap and decreasing fill. A value of 0 indicates no nestedness and 100 indicates perfect nestedness. The metric is not related to network size (Almeida-Neto et $al.$, 2008).

Additional network-level indices were calculated. Quantitative linkage density measures the diversity of interactions per species weighted by the marginal totals (Bersier et $al.$, 2002). Interaction strength asymmetry (ISA) is another measure of specialization across both trophic levels which quantifies the average effect of each species on all its partners; positive values indicate higher dependence of the higher trophic level, in this case animal pollinators (Blüthgen et $al.$, 2007).

Alongside these network-level indices, the standardized specialization index d' as described in Blüthgen et $al.$ (2006) was calculated to evaluate the specialization of individual taxonomic groups in the network. Let p_{ij}' equal the proportion of interactions between a plant i species and an animal pollinator j species compared to the row total of interactions, and q_j equal the proportion of interactions by species j in relation to the total number of interactions. The specialization of a given species i is given as

$$d_i = \sum_{j=1}^{c} (p_{ij}' \times \ln\left(\frac{p_{ij}'}{q_j}\right))$$

Thus, d accounts for the number of interactions with each partner given overall partner availability, q_j. d is then normalized to d' and ranges from 0 for the most generalized case to 1 for the most specialized. d' was only calculated for the animal and plants of the pooled-taxa matrix. Calculation at the taxa level more adequately accounts for generalization, as a plant species that is pollinated by many species of the same family may be inaccurately regarded as more generalized as a plant pollinated by species of a wide array of taxa (Johnson & Steiner, 2000). This index was calculated using the 'dfun' function of the bipartite package.

Evaluating sampling efforts

Given the limited time under which data was collected, sampling effort was considered by creating a species rarefaction curve using the iNEXT package (Hsieh et $al.$, 2016). Sampling effort was measured as the number of animal pollinators collected and assumes that more observation time would lead to a higher abundance of pollination events observed.

Ethics

Observations were conducted on land owned by the EcoMinga foundation, adjacent to the Río Zuñac Reserve. The transect was set up on the existing trail, so no plants were disturbed in the process of observation. In order to identify animals, insects were caught and placed in alcohol for identification with a microscope. Animals that did not have to be seen with a microscope to be identified, such as butterflies or insects that were clearly the same morphospecies, were not placed in alcohol. The insects that were killed represent an insignificant portion of the total insect pollinators in the cloud forest. This study did not involve human subjects.

Results

Of the 39 species of flowering plants observed in the transect, 20 species received pollination visits. 115 animal pollinators were observed, with 40 unique species of animal pollinators identified over 26.5 hours of sampling. Animal pollinators were grouped into 10 taxonomic groups: four orders (Diptera, Coleoptera, Hymenoptera, and Lepidoptera) and six families (bees; Apidae, Halictidae, Andrenidae, and Megachilidae, in addition to Trochilidae and Syrphidae). The size of the species-level matrix was 800, and the size of the taxa-level matrix was 200.

The most abundant pollinator species was *Trigona sp1* (family Apidae) with 20 individuals, followed by *Empididae sp3* (order Diptera) with 11 individuals. 19 pollinator species were observed only once, and 32 species were observed less than five times. The most abundant taxonomic groups were Apidae with 34 individuals and Diptera with 31 individuals, followed by Lepidoptera with 15 individuals. The least observed taxonomic groups include the remaining bee families: Halictidae with 1 individual and Andrenidae and Megachilidae with 2 individuals each.

50 unique interactions were observed between animal pollinators and flowering plants in the species-level matrix (Figure 4a, Figure 5a). Figure 5 visualizes the interaction strength between mutualist partners as represented by interaction frequency. Connectance C is 0.0675. The measure of network-level specialization H_2' is 0.78 (Figure 4a). ISA is 0.23. The quantitative linkage density is 2.24. NODF is 3.59. Figures 4b and 5b present the network with animal pollinators grouped as taxa. The plant species *Glossoloma tetragonoides* and *Clibadium sp* had the highest number of interactions with potential pollinators, as visualized by the size of their bars (Figure 4).
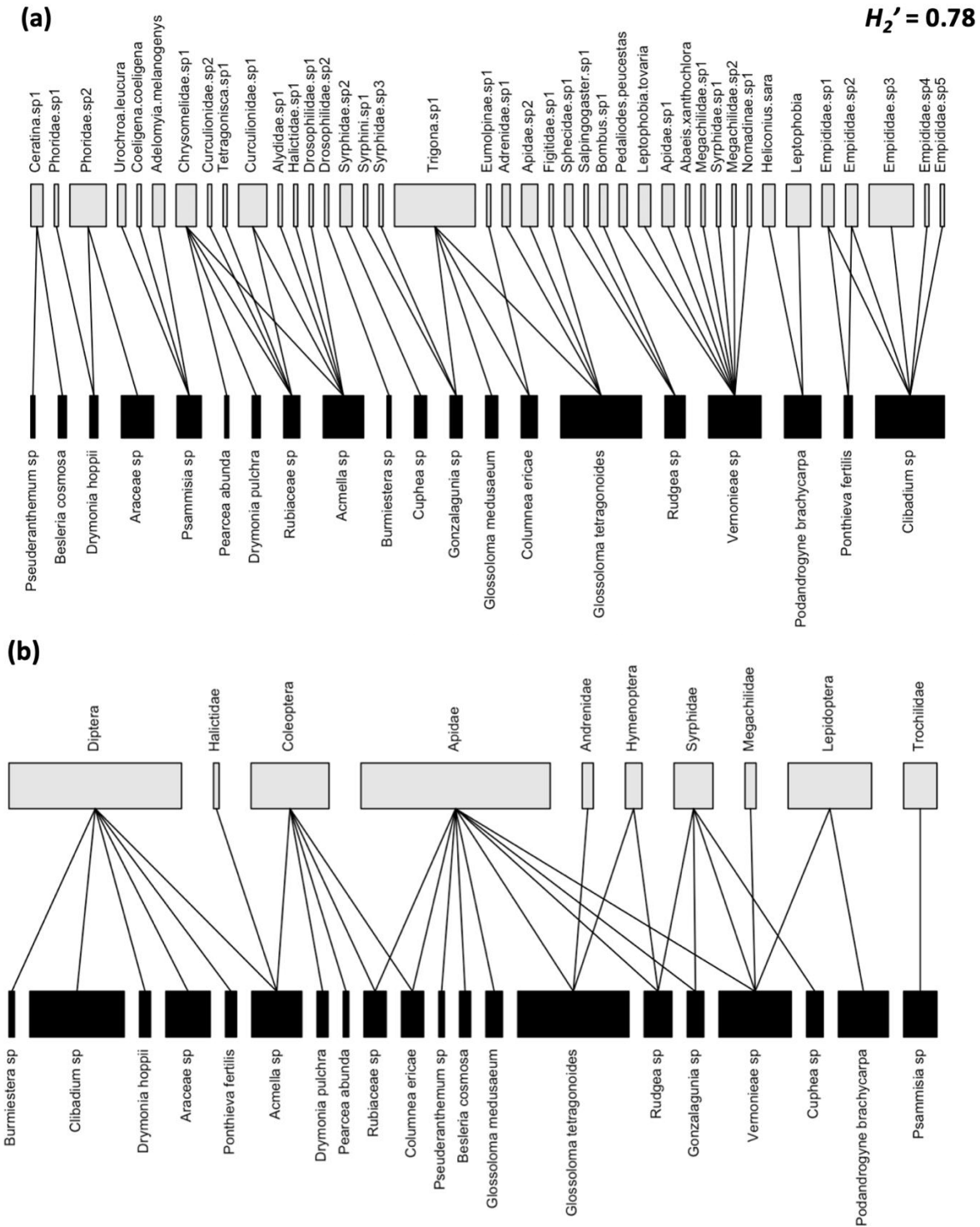
Figure 4. Plant-pollinator network in a secondary forest near the Río Zuñac reserve represented as bipartite web. The bottom bars represent flowering plant species. The top bars in (a) represent animal pollinator morphospecies and in (b) represent pollinator families or orders. H_2' is given for (a) to indicate the specificity of network interactions. The size of the bar increases with the number of interactions the species has. Unique interactions, in this case pollination events, are represented by lines between pollinators and plants.

(a)

(b)
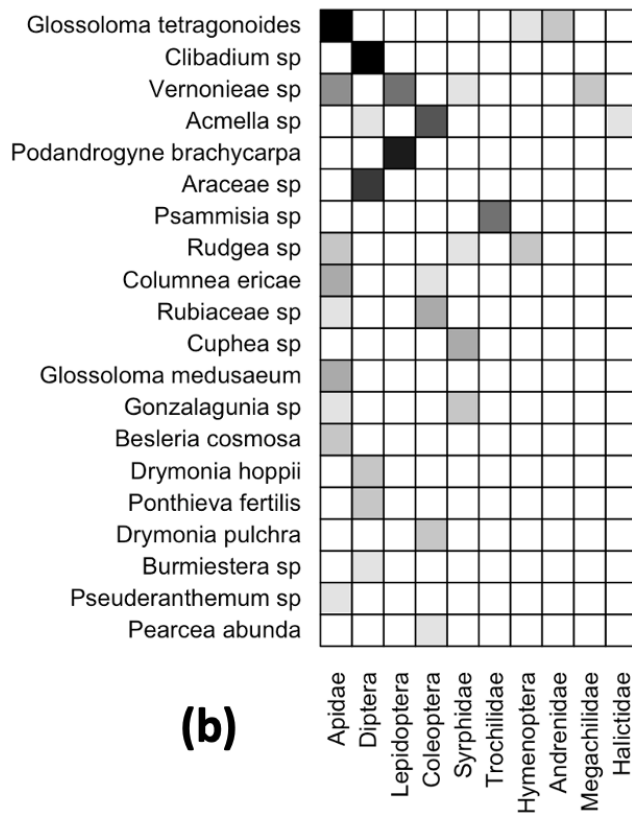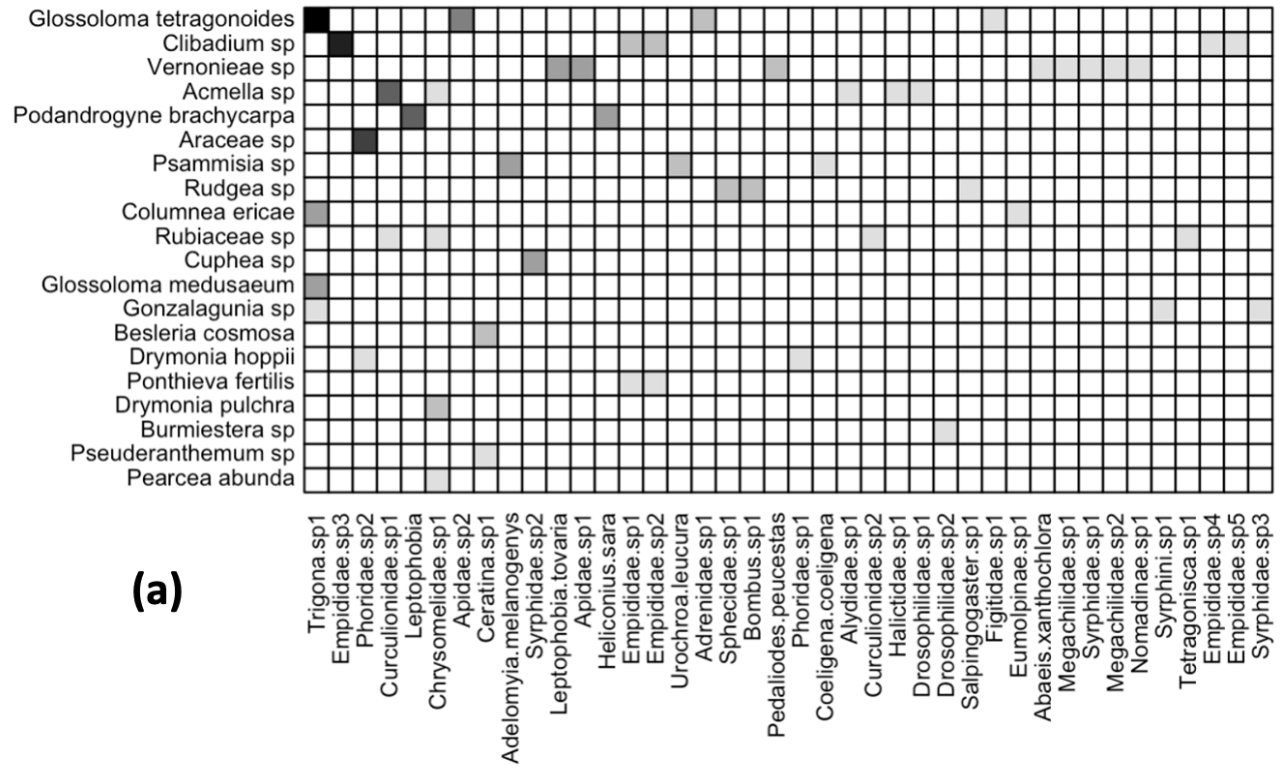
Figure 5. Plant-pollinator network represented as matrix. Plant species are rows. In (a), columns are animal pollinator morphospecies, and in (b), columns are animal pollinator taxa. Shaded squares represent interactions between plant and pollinators. Darker squares indicate a higher frequency of interaction.

Table 1. *d'* values generated from pooled-taxa matrix for each plant species.

Plant species	d'
Glossoloma tetragonoides	0.026
Burmeistera sp	0.026
Pseuderanthemum sp	0
Besleria cosmosa	0.186
Drymonia hoppii	0.212
Psammisia sp	1
Acmella sp	0.621
Cuphea sp	0.737
Rudgea sp	0.417
Glossoloma medusaeum	0.247
Columnea ericae	0.194
Vernonieae sp	0.412
Araceae sp	0.464
Gonzalagunia sp	0.376
Rubiaceae sp	0.338
Podandrogyne brachycarpa	0.79
Ponthieva fertilis	0.212
Clibadium sp	0.675
Pearcea abunda	0.252
Drymonia pulchra	0.441

Table 2. d' values generated from pooled-taxa matrix for each taxonomic group of animal pollinators.

Taxon	d'
Apidae	0.682
Diptera	0.943
Trochilidae	1
Coleoptera	0.848
Halictidae	0.267
Syrphidae	0.701
Andrenidae	0.21
Hymenoptera	0.425
Lepidoptera	0.831
Megachilidae	0.358

d' values were calculated for 20 species of plants and 10 taxonomic groups of animals. Both plants and animals have a wide range of d' values. For plant species, d' values range from 0 to 1, which represent extreme generalization to extreme specialization (Table 1). The average d'

value for plants is 0.381. The species with the highest number of interactions with potential mutalists, *G. tetragonoides* and *Clibadium sp,* have d' values of 0.026 and 0.675, respectively. For animal taxa, d' values range from 0.21 to 1 (Table 2). The average d' for animal taxa is 0.626. The most abundant animal taxa, Apidae, Diptera, and Lepidoptera, have d' values that are higher than the average.
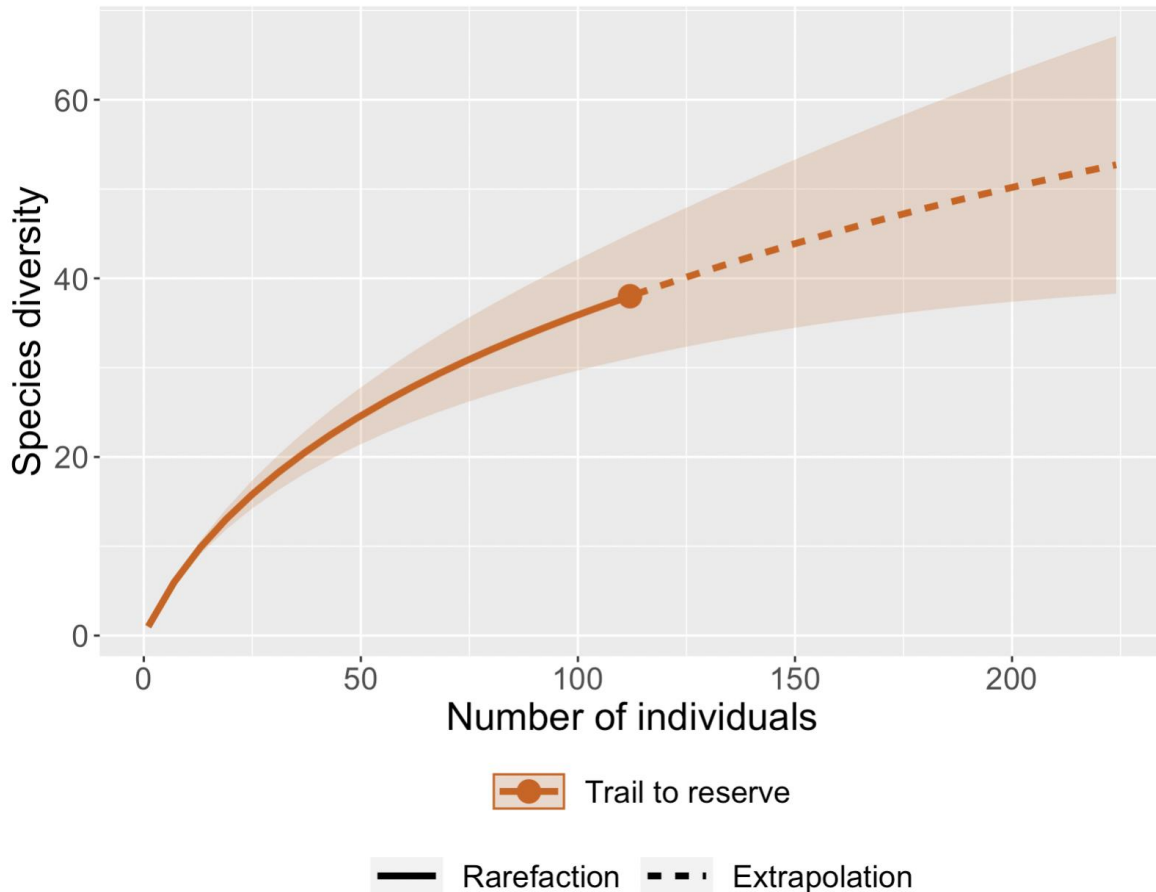
Figure 6. Species rarefaction curve for sampling efforts along transect given 26.5 hours of observation.

19 species of flowering plants did not receive any pollination visits. Some of these species were rare in the transect or flowered at the end of the dates allocated for observation and thus were observed only a few times. The average observation time for a plant species that received pollination visits was 55 minutes, whereas the average time for a plant species that did not receive pollination visits was 23 minutes. Of the species that did not receive any pollination visits, five were observed for more than 45 minutes. A species rarefaction curve was calculated to evaluate sampling efforts based on the number of animals collected (Figure 6). More sampling would continue to reveal more species of floral visitors. Assuming the same rate of animal collection per unit time, doubling the observation time would yield 52 species of animal pollinators, as compared to 39 species collected during the study.

Figure 7. Photos of *Trigona sp1* visiting flowers of *Glossoloma medusaeum* (left) and *Glossoloma tetragonoides* (right).

The behavior of *Trigona sp1*, the most abundant pollinator, was documented. An individual would land on a flower and crawl under the bract, presumably to access the nectar from the base of the flower (Figure 7). The individual did not appear to be in contact with the reproductive parts of the flower but this study it is considered as a potential pollinator. This interaction happened more than once, but individuals were also observed to enter the flower and touch the reproductive parts inside. These interactions were observed on three species of the Gesneriaceae family, *Glossoloma medasaeum, Glossoloma tetragonoides,* and *Columnea ericae.*

Analysis and Discussion

Analysis of pollination networks yield powerful insights into the characteristics of network-wide interactions. This study reveals that there is a diverse set of animal pollinators interacting with flowering plants and that the interactions are more specialized than generalized.

Connectance decreases with network size and is strongly affected by sampling effort (Goldwasser & Roughgarden, 1997) and thus may not always used to explain network structure without accounting for network size (Olesen & Jordano, 2002). The low value of connectance is best understood in relation to the relatively high value of network-level specialization. H_2' is not correlated to network size, allowing for comparisons between networks because species-rich and species-poor networks do not differ inherently in network-level specialization (Blüthgen *et al.,* 2007). Considering pollination networks on a spectrum of specialization to generalization, both values indicate that this network is more specialized. The H_2' is higher than those found in studies of temperate systems (Fründ *et al.,* 2010; Michelot-Antalik, 2021). These results agree with Cuartas-Hernández *et al.* (2015), which found that in small network units sampled at a specific time and altitude, as was done with this study, most species interacted with only one other species. If samples are taken at different times, it is possible to find that plants and pollinators interact with a wider group of mutualist partners when their phenologies overlap, which could not be seen during the short observation period of this study. As observed here, pollination networks in a given time and space are relatively specialized at the network-level.

This network had a low degree of nestedness. Although some metrics of nestedness are affected by high species richness (Bascompte *et al.,* 2003), the NODF metric used in this study is not affected by matrix size (Almeida-Neto *et al.,* 2008). Highly nested networks may better be able to respond to perturbations and provide routes for rare species to persist (Bascompte *et al.,* 2003). Even with high degrees of specialization, nested networks are better able to resist collapse when confronted with species extinction because of redundancy in network interactions (Memmott *et al.,* 2004). The implications are that a non-nested network is more susceptible to the elimination of any one species, although these effects would be constrained to the mutualist partners of that species.

All network-level and taxon-level indices should be considered in light of the low number of potential animal pollinators observed in this study. 115 potential pollinators were documented representing 40 species, with almost half of all species being represented by only one individual. There were fewer than five interactions that represented almost all links between species. More sampling effort would have yielded a higher number of animal pollinators, increasing the number of interactions present in the network. Any interaction in the present matrix represents a comparatively large portion of total interactions of that species. Given the low number of interactions, increased sampling effort would have also increased the descriptive power of the indices by providing more detailed insight into interaction strength and reducing the impact of any one species. The species rarefaction curve also shows that there are likely more animal species interacting in the network that would be identified with more observation time. Many observation hours of this study were conducted in cloudy weather with low sun intensity because of the erratic and brief hours of sunlight, which reduced pollination visits (Watson *et al.,* 2022). Although it remains unclear the extent to which sunlight intensity impacted pollinator abundance, focusing observation time on the available hours of sunlight may yield a more representative sampling of pollinators.

The effects of the low number of interactions recorded are best observed in the values of d' calculated for individual species and taxa. *Pseuderanthemum sp* had a d' value of 0 despite only having one mutualist partner. The interaction frequencies in the matrix were sufficiently low to render the descriptor power of d' void for some species and taxa, such as *Pseuderanthemum*. d' may be more appropriately considered for species and taxa that have a larger number of interactions. When comparing the most abundant taxa, Diptera and Lepidoptera have higher specialization values than Apidae, although all had values of d' above 0.5. These taxa were abundantly sampled interacting with only a few plant species. These values indicate that in a given time, pollinators interact with a small number of mutualist partners. This also highlights the importance of Apidae pollinators in the network as they are abundant and fairly generalized when compared to other abundant taxa.

This plant-pollinator network is characterized by a high richness of animal pollinators compared to plants. This asymmetrical network is expected of pollination networks, which tend to have more animal pollinators than plants (Blüthgen *et al.,* 2007). The positive ISA value of 0.23 indicates that individual animal pollinator species are more dependent on plant species than plant species are on animal pollinators. Animal pollinator species interact with comparatively fewer species of flowering plants and are thus more specialized than plant species. This reveals the importance of floral diversity in supporting a high richness of animal pollinators. Only two out of 39 species of animal pollinators visited more than two species of plants, while eight out of 20 species of plants were visited by more than two species of insects. The absolute value of asymmetry is relatively low, meaning that the differences in specialization between animals and

plants is not large. Network architecture places restrictions on specialization; with fewer potential plant mutualist partners, animal pollinators interact with a greater proportion of available partners and tend to be more generalized (Blüthgen *et al.,* 2007). This network had a higher degree of animal specialization despite a higher animal species richness. According to an analysis of pollination networks, animal pollinators are more specialized than expected by network architecture (Blüthgen *et al.,* 2007), which agrees with the findings of this study.

This study did not consider nocturnal pollination. Bats are pollinators of hundreds of species in the Neotropics (von Helverson & von Helverson, 1999). Plants in this system may have been pollinated by bats. For example, the *Burmeistera* genus seems to ascribe to the chiropterophilous syndrome and has been shown to be pollinated by bats in Ecuadorian cloud forests (Mucchala & Jarrín-V, 2002). Additionally, this study did not consider pollination networks across spatial or temporal scales. Changes in altitude and time, especially across rainy and dry months, impacts the availability of floral resources, which significantly affects the richness of floral visitors (Cuartas-Hernández & Gómez-Murillo, 2015). Montane pollination networks have been shown to have high species turnover across time and small altitudinal gradients (Cuartas-Hernández & Medel, 2015). Severe abiotic conditions, such as those found at high elevations, may affect measures of network topology, like nestedness (Ramos-Jiliberto *et al.,* 2010). Therefore, expanding the spatial scale of the present study to include different altitudes would yield useful insights into the role of abiotic conditions in shaping the topology of pollination networks and inform conservation priorities. Increasing the temporal scale of observation would help build a more robust understanding of cloud forest pollination networks. Considering the variable phenology of plants and pollinators and the wide range of altitudes, the present study is best understood as a snapshot of the pollination network in the eastern Ecuadorian cloud forest.

There are biotic factors that are relevant in pollinator ecology that were not included in this study. The metric used for interaction strength in this study, interaction frequency, does not account for the efficiency of pollination. In ecological terms, the purpose of flower specialization in mutualistic interactions is to interact with effective pollinators. Although specialized flowers may receive visits from a wide assemblage of opportunistic floral visitors, only a fraction of these may act as effective pollinators (Ollerton, 1996; Schemske & Horvitz, 1984). When pollination network analysis looks at a larger group of generalized interactions, it might not show how important more specific pollination interactions are for the plants' ability to reproduce. Certainly, even as reviews of global pollination networks report only a marginal decrease in connectance, meaning an increase in specialization, in tropical systems (Olesen & Jordano, 2002), a study of pollination systems in lowland tropical forests found that only 37 out of 270 species were considered to have diverse pollination syndromes (Momose *et al.,* 1998).

The case of *Trigona sp1*, the most abundant pollinator in this network, provides useful insights into the consideration of the effectiveness of pollination interactions not accounted for in the present approach. This species was observed crawling under the bracts of certain flowers. This behavior may be consistent with nectar robbery, when nectar is removed through a hole made in the corolla (Maloof & Inouye, 2000), although the flowers were not inspected at the time for any holes. Nectar robbers may also act as pollinators (Sampson *et al.,* 2004; Maloof & Inouye, 2000), although this could not be verified within the limits of this study. *Trigona* species have been documented as nectar robbers with negative impacts on plant seed sets because of their territorial behavior (Roubik 1982). More investigation into the behavior of *Trigona sp1* and the seed set of the plants with which it interacts is needed before concluding its effects on

pollination. Accounting for the efficiency of pollination, while an important next step in the study of mutualistic networks, presents a considerable challenge in the already intensive task of observing pollination networks.

Considering the general lack of literature on tropical cloud forests, this study presents an introductory understanding of the metrics of specialization and identification of mutualist species in cloud forest pollination networks. Further investigation into the crucial ecosystem dynamics of cloud forests is needed to help inform conservation efforts. Understanding the diversity and robustness of pollination networks will help guide the conservation and protection of pollination services and help prioritize the protection of important plant and pollinator species.

Conclusion

This study investigated the assemblages of plants and potential pollinators in the eastern Ecuadorian cloud forest. A high species richness of flowering plants and potential pollinators interacting in a network was documented within the spatial and temporal limitations of observation. The most abundant pollinator groups, Apidae, Diptera, and Lepidoptera tended to be more specialized; the comparatively lower degree of specialization of Apidae marks this family as important network-level pollinators. Interaction asymmetry reveals that animals tend to be more specialized than plants and highlights the importance of plant species in maintaining a diverse assemblage of pollinators. Network-level specialization was relatively high, and there was a low level of nestedness, indicating that the network may be comparatively more vulnerable to species extinctions of mutualist partners than highly nested networks. This study, undertaken within a single altitude and time of year, represents a snapshot of cloud forest pollination networks, which likely change in species assemblages and other network indices throughout spatial and temporal scales. More investigation, especially across temporal and spatial scales, is needed to better understand the dynamics of pollination networks in the Río Zuñac reserve. Considering the diverse assemblage of mutualist partners and relatively high specialization, the integrity of cloud forest pollination networks appears to be susceptible to factors that can lead to local extinctions of mutualist partners, such as habitat destruction or degradation that threaten cloud forest ecosystems.

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Appendix

Appendix A. Frequency based matrix of plant and potential pollinator interactions. Plant species indicated as P1 (Glossoloma tetragonoides), P2 (Burmeistera sp), P3 (Pseuderanthemum sp), P4 (Besleria cosmosa), P5 (Drymonia hoppii), P6 (Psammisia sp), P7 (Acmella sp), P8 (Cuphea sp), P9 (Rudgea sp), P10 (Glossoloma medusaeum), P11 (Columnea ericae), P12 (Vernonieae sp), P13 (Araceae sp), P14 (Gonzalagunia sp), P15 (Rubiaceae sp), P16 (Podandrogyne brachycarpa), P17 (Ponthieva fertilis), P18 (Clibadium sp), P19 (Pearcea abunda), P20 (Drymonia pulchra).

Animal species	Animal taxa	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	P16	P17	P18	P19	P20
Ceratina sp1	Apidae	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phoridae sp1	Diptera	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phoridae sp2	Diptera	0	0	0	0	1	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0
Urochroa leucura	Trochilidae	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coeligena coeligena	Trochilidae	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adelomyia melanogenys	Trochilidae	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chrysomelidae sp1	Coleoptera	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	2
Curculionidae sp1	Coleoptera	0	0	0	0	0	0	6	0	0	0	0	0	0	0	1	0	0	0	0	0
Curculionidae sp2	Coleoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Halictidae sp1	Halictidae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Drosophilidae sp1	Diptera	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Drosophilidae sp2	Diptera	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Syrphidae sp2	Syrphidae	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Trigona sp1	Apidae	13	0	0	0	0	0	0	0	0	3	3	0	0	1	0	0	0	0	0	0
Apidae sp2	Apidae	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Andrenidae sp1	Andrenidae	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphecidae sp1	Sphecidae	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Salpingogaster sp1	Syrphidae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Bombus sp1	Apidae	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Figitidae sp1	Figitidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eumolpinae sp1	Coleoptera	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Pedaliodes peucestas	Lepidoptera	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Leptophobia tovaria	Lepidoptera	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
Apidae sp1	Apidae	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
Abaeis xanthochlora	Lepidoptera	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Megachilidae sp1	Megachilidae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Syrphidae sp1	Syrphidae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Megachilidae sp2	Megachilidae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Nomadinae sp1	Apidae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Syrphini sp1	Syrphidae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Tetragonisca sp1	Apidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Heliconius sara	Lepidoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
Leptophobia	Lepidoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0
Empididae sp1	Diptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0
Empididae sp2	Diptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0
Empididae sp3	Diptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0

Empididae sp4	Diptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Empididae sp5	Diptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Syrphidae sp3	Syrphidae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0