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Structural Responses to Land Use in Pollination Networks: Effects of Biodiversity and Alien Plants in the Ecuadorian Chocó

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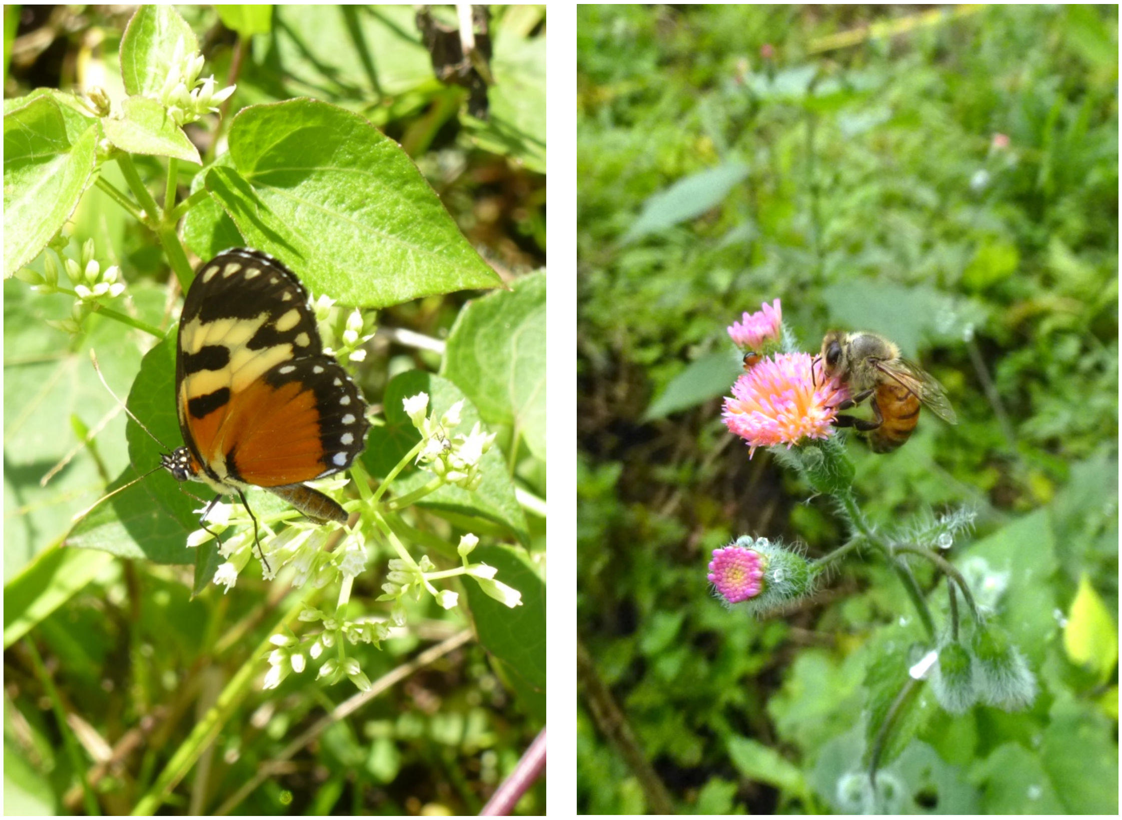
Structural Responses to Land Use in Pollination Networks:

Effects of Biodiversity and Alien Plants in the Ecuadorian Chocó



(Left) *Eresia ithomoides* pollinates *Mikania micrantha*. (Right) *Apis mellifera* pollinates *Emilia sonchifolia.* Photos by author.

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Río Manduriacu Valley
Cotacachi Canton, Imbabura Province, Ecuador

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Abstract

As a globally recognized hotspot of biodiversity, the Ecuadorian Chocó Andino region is extremely important for research and conservation. However, little research has been done regarding the mutualistic networks that sustain this ecosystem. The analysis of plant-pollinator networks helps us understand how ecosystems respond to change and is vital to conserving ecological productivity across multiple spatial scales. This study establishes a baseline for pollinator network structure across a land use gradient near the western montane cloud forest in Ecuador. Plants and pollinators were sampled along 11 transects in farms, communities, roads in the Río Manduriacu valley. Weedy herbs dominated overall, with exotic ornamentals playing an important role in the "town" network. Hymenoptera was the most abundant pollinator order in all networks, followed by Lepidoptera and Diptera. Plant richness and pollinator richness showed opposite distributions between the habitats, indicating asymmetry between trophic levels. Connectance was low in all networks, complemented by high levels specialization. The "farm" network was the most nested and most robust to secondary extinctions, indicating more network stability in agricultural areas. Non-native plants generally overperformed native plants for partner diversity, and non-native pollinators were central to network structure. These results indicate that land use has a destabilizing effect on pollinator networks and facilitates invasions of alien plants and pollinators. Although more research is needed to inform specific restoration proposals, this study reveals an urgent need for pollinator habitat enhancement in disturbed areas of the Chocó Andino to protect biodiversity and provide benefits to nearby communities.

Resumen

El Chocó Andino ecuatoriano es un hotspot de biodiversidad y es sumamente importante para la investigación y conservación. Sin embargo, se ha realizado poca investigación sobre las redes mutualistas que sostienen este ecosistema. El análisis de las redes de polinización nos ayuda a endender cómo responden los ecosistemas a las perturbaciones y es vital para conservar la productividad ecológica en varias escalas espaciales. Este estudio estableció una línea base para la estructura de las redes de polinización a través de un espectro de usos de la tierra cerca del bosque nublado occidental en Ecuador. Se muestrearon plantas y polinizadores a lo largo de 11 transectos en fincas, comunidades y vías en el valle del Río Manduriacu. Las malas hierbas dominaron en general, y las plantas ornamentales exóticas desempeñaron un papel importante en la red de "pueblo". Hymenoptera fue el orden de polinizadores más abundante en todas las redes, seguido por Lepidoptera y Diptera. La riqueza de plantas y la riqueza de polinizadores mostraron distribuciones opuestas entre los hábitats, indicando asimetría entre los niveles tróficos. La conectividad fue baja en todas las redes, complementada por altos niveles de especialización. La red de "fincas" fue la más anidada y robusta ante extinciones secundarias, indicando una mayor estabilidad de la red en áreas agrícolas. Las plantas no nativas generalmente superaron a las plantas nativas en diversidad de parejas, y los polinizadores no nativos fueron centrales en la estructura de la red. Estos resultados indican que el uso de la tierra tiene un efecto desestabilizador en las redes de polinizadores y facilita las invasiones de plantas y polinizadores no nativos. Aunque se necesita más investigación para informar propuestas de restauración específicas, este estudio revela una necesidad urgente de mejorar los hábitats de polinizadores en áreas perturbadas del Chocó Andino para proteger la biodiversidad y proporcionar beneficios a las comunidades cercanas.

Introduction

It's well-established that various human land uses cause biodiversity loss and the disruption of ecological processes (Millard et al., 2021). In Ecuador, and in the tropics in general, habitat destruction is a widespread and accelerating phenomenon. Natural resource exploitation, farming and ranching, and urbanization are the main causes of this trend (Ríos-Touma et al., 2022). In response, a growing network of conservation areas, reserves, and national parks have emerged, covering around 20% of the country's area in total (Kleemann et al., 2022). Despite seemingly robust conservation efforts, Ecuador holds second place globally for quantity of threatened species and has the highest percentage of protected areas bordered by infrastructural development in South America (Andrade-Núñez & Aide, 2020). Although reserve boundaries are significant for determining limits of human land use, the actual extent of ecosystems – whether defined by species ranges, topographic barriers, or other natural features – rarely fit cleanly within designated protected areas (DeFries et al., 2007). For this reason, it's essential to understand how ecological processes may spill over and change in these natural-altered habitat interfaces. It's equally important to understand how specific land use types affect the structure and functioning of these processes on various scales.

Pollination is a prime candidate for this kind of analysis, as the diversity and abundance of animal pollinators are dramatically affected by land use intensity (Millard et al., 2021). The global decline of pollinators in recent decades has been largely attributed to anthropogenic environmental change, and is of great concern for biodiversity loss, food systems, and global ecosystem functioning (Potts et al., 2010). Land use impacts pollinators both indirectly through changes in floral composition and abundance, and directly through life cycle disruption, contamination, or nesting habitat destruction (Weiner et al., 2014). In the tropics, the vast majority of flowering plants rely on animal pollinators to reproduce, leading to the creation of complex plant-pollinator networks (Vizentin-Bugoni et al., 2018). These networks are ecosystem-scale amalgamations of individual plant-pollinator mutualisms and are of utmost importance for the development and maintenance of local biodiversity. They also provide benefits to farmers by boosting yields for animal-pollinated crops (Young et al., 2021). Analyzing pollination with a network approach reveals large-scale patterns that allow for comparative study between habitats, informing conservation, restoration, and land management (Bascompte, 2009).

At their most basic, a pollination network is a bipartite network where nodes are separated into two independent and non-overlapping sets (Dormann et al., 2009). These sets are plant species (the lower trophic level) and pollinator species (the higher trophic level). Network edges represent the mutualistic interactions between plants and pollinators, and can only connect nodes in one set with nodes in the opposite set (see Figures 4a-4c). In addition to this fundamental structure, researchers have proposed numerous statistical variables that control or describe the organization of a network. These variables include the number of connections, the degree of specialization in the network, and the redundancy of interactions. Network-level analysis of this kind can reveal useful information about the robustness of networks to extinction cascades and can link network structure to real-world environmental conditions (Fortuna et al., 2010). Pollination networks can also be analyzed on a species level, allowing for insight into species' characteristics and their respective contributions to the network (Arroyo-Correa et al., 2021). Some important species-level variables include the number of partner species per species and the centrality of each species in the network. These analyses have important conservation implications, as they can help identify keystone species within the network in both trophic levels (Crespo Ampudia et al., 2021).

Previous studies have analyzed how network structure is affected by biotic and abiotic conditions in relatively undisturbed ecosystems in Ecuador (Diaz, 2023; López-Ruiz, 2023; Crafford, 2020). However, few studies have explored pollination ecology across different human land uses in the country. Just as plant and pollinator populations are disrupted by habitat modification, the structure of plant-pollinator networks is also sensitive to land use (Ferreira et al., 2013). Habitat fragmentation creates parallel declines in plant and pollinator diversity, with specialist species facing higher vulnerability than generalists (Weiner et al., 2014). This can lead to simplified networks flooded with cosmopolitan generalists. In addition, introduced or invasive exotic plants, which are common in human-modified habitats, have caused numerous changes to network stability and complexity in previous studies (Zaninotto et al., 2023). For example, increased competition from alien plants can lead to declines in pollinator visitation for native plants and heterospecific pollen transfer that limits plant reproductive success across the network (Parra-Tabla & Arceo-Gómez, 2021; Marrero et al., 2017). However, the effects of changing environmental conditions on pollination networks are not globally consistent. The unique climate and high endemism of the Andean cloud forest in Ecuador make its pollinator networks distinct from temperate zones, where most research on this subject has been conducted. For this reason, any efforts to boost plant-pollinator diversity and/or robustness in this area must be informed by local science.

The immense economic, biological, and cultural importance of these forests and surrounding areas, known collectively as the Chocó Andino biogeographical region, creates urgent need for ecological research and conservation. This ecozone spans over 15,000 km^2 along the western foothills of the Ecuadorian Andes, connecting with a larger ecosystem that extends into western Colombia and Panamá (Ron, 2020). Over half of the forests of this region have been removed or fragmented to make way for human settlement, agriculture, cattle ranching, and mining projects (Ocaña Zambrano et al., 2021). This deforestation severely limits the provisioning of ecosystem services to nearby communities, including fresh water, soil stability, and most relevant to this study, pollination. Numerous articles have indicated landscape-scale drivers of pollinator abundance and diversity in other parts of the world. This means the configuration and quality of habitat fragments across a disturbed landscape may directly affect pollination services (Gillespie et al., 2022). However, little research has been done regarding the status of pollination networks in human-modified areas of the Chocó Andino. Since communities in this region rely heavily on artisanal agriculture for income, much of which involves crops that are animal-pollinated, it's vital to understand how anthropogenic disturbance influences plant-pollinator assemblages across a spectrum of land uses.

This study aims to quantitatively compare plant-pollinator networks across agricultural, populated, and roadside habitats in the Chocó Andino ecoregion of Ecuador. In pursuing this objective, the author proposes the following sub-questions:

- What are the effects of alien plant invasions on network characteristics?
- Which network characteristics have the strongest impact on pollinator robustness?
- Do certain pollinators have an outsized contribution to network structure and functioning?

Answering these questions will provide useful insight into the dynamics of pollinator networks in disturbed areas, which is still a developing field of study within ecology. In addition, this study will provide locally applicable conservation recommendations that have the potential to increase both local biodiversity and crop yields through more effective pollination.

Methods

Study site

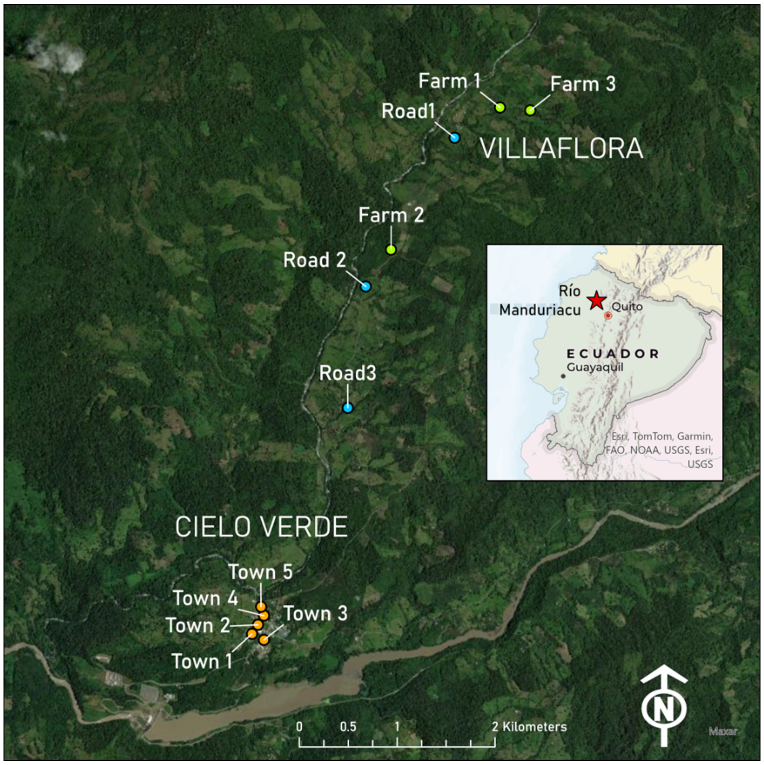


Figure 1. Map of study site including transect location and site location within Ecuador. Made using ArcGIS Pro Version 3.2 (ArcGIS Pro, 2023).

Research was conducted in the Río Manduriacu valley in Cotacachi Canton, Imbabura Province, Ecuador. Situated in the western Andean foothills, this site is part of the Chocó Andino ecoregion, which is known worldwide as a hotspot of endemism and biodiversity (Cuesta et al., 2017). This region is also marked by moderately intensive yellow pitahaya (*Selenicereus megalanthus*) and plantain (*Musa sp.*) cultivation, as well as cattle ranching in lowland areas. Upland areas are mostly undisturbed or secondary cloud forest. The Río Manduriaco Reserve, owned and operated by Fundación EcoMinga, protects over 600 hectares of this forest habitat (Fundación EcoMinga, 2018). Data collection occurred between May 15 and May 30, 2024, during a period of El Niño. This climatic anomaly created unusually dry conditions and likely induced changes in plant phenology that led to a lack of understory flowers in primary and secondary forest (Flores et al., 2023). For this reason, data was only collected in human-modified habitats. 11 transects were surveyed, each with a length of 25 or 50 meters, depending on floral composition and spatial limitations. Transect locations were chosen with the permission of landowners and by rapidly assessing the presence of flowers and accessibility of each site. Three agricultural transects were conducted in farms near the community of Villaflora de Manduriacu, either within or adjacent to plantain or dragon fruit crops. Farms were generally located at the base of slopes, with forest fragments found further uphill. Many local farmers actively control wild plant growth in their fields with herbicide, which leads to an absence of flowers. For this reason, farm transects were only conducted in fields that had not recently been treated. Five community transects were conducted in gardens, green spaces, and vacant lots within the town of Cielo Verde, near the

Manduriacu River Hydroelectric Dam. Finally, three road transects were surveyed along the margins of the 6.5-kilometer unpaved route connecting the communities of Villaflora and Cielo Verde. This road covers a roughly 300-meter elevation difference, with Cielo Verde at 600 meters above sea level, and some farms in the upper portion of the valley reaching over 900 meters above sea level. Average temperature varies across the elevation gradient, generally falling between 16ºC and 19ºC in May. The monthly precipitation average is 500 millimeters, with sunny or overcast mornings and rainy afternoons (Climate Data, 2021).

Figure 2. Transect sites. Left: transect 2, farm; Middle: transect 4, town; Right: transect 9, road. Photos by author.

Field Sampling

Pollinator surveys took place in the mornings between the hours of 8:00 am and 12:00 pm, in order to synchronize sampling with pollinator temporal patterns and flower opening times (Cox & Gaston, 2024). Specific dates and times for data collection were weather-dependent; all transects were surveyed in sunny or cloudy weather, and collection stopped if it began to rain. A 70-meter measuring tape was used to set up each transect. Sampling occurred on both sides of the transect, extending one meter laterally in either direction (López-Ruiz, 2023). Work began with a basic floristic survey, photographing each plant species with active flowers along the transect. For abundant plant species, only five individuals were sampled, in order to avoid bias in the network based on local-scale plant community structure. After the floristic survey, each transect was walked again, observing each selected flowering plant individual for five minutes.

Any pollinators that visited the selected flowering plants during the observation period were subsequently collected and/or photographed, and the frequency of each plant-pollinator interaction was recorded. Photos of plant and animal samples were taken with a Panasonic Lumix digital camera. Collection of certain Hymenopterans and Dipterans was conducted with an aspirator, pincers, and/or butterfly net, depending on morphology. All Lepidopterans were photographed in the field. Insects were identified as pollinators, i.e. distinguished from other floral visitors, when their mouthparts were observed touching floral reproductive structures for more than three seconds. With one exception, insects that weren't members of the Lepidoptera (butterflies and moths), Diptera (flies), Coleoptera (beetles), or Hymenoptera (ants, bees, and wasps) orders were not considered pollinators (Grange et al., 2021). Insect samples were collected in zip-top plastic bags and brought to the lab. Samples were placed in a home freezer for three minutes induce torpor. Insects were then quickly photographed and flew away once they awoke. Total sampling time across all transects was 27 hours, with a range of 5-95 minutes of observation per plant species.

Samples were identified using the iNaturalist app's suggestions, verified using a wide array of online resources, as well as community input from iNaturalist users (*iNaturalist Ecuador*, 2024). All samples were identified to the lowest taxonomic rank possible, and plants were categorized as native or non-native using the Missouri Botanical Garden's "Tropicos" web catalogue (Jørgensen, 2009). Any inconclusive samples were sent to experts for more accurate identification. Ricardo Zambrano-Cevallos assisted with plant identification, Dr. Xavier Silva assisted with lepidopteran identification, and Ana María Ortega assisted with all other insect identification.

Data Analysis

Data were analyzed using R version 4.3.1 (R Core Team, 2023). Transect data was combined by habitat to construct three matrices for network analysis: "Farm", "Town", and "Road". Each matrix was structured with pollinator species listed in columns and plant species in rows. The cells within the matrix represented the counts of observed interactions between respective pollinator and plant species pairs. In order to assess the relationship between sampling effort and diversity between the habitats, the "iNext" package was used to extrapolate plant and pollinator species richness to 200 samples based on a rarefaction curve (Hsieh & Chao, 2024). Relative abundances of plant families and insect orders were calculated using plant-pollinator interaction frequency data. Beta plant and pollinator diversity (β) between the three habitats was calculated as pairwise Sørensen dissimilarity using the "betapart" package in R (Baselga et al., 2023). Dissimilarity values were then inverted to obtain percent overlap between each plot. Where a is the number of species shared between sites 1 and 2, b is the number of species that are unique to site 1, and c is the number of species unique to site 2, beta diversity (β) is given as:

$$\beta = 1 - (\frac{b + c}{2a + b + c})$$

The "bipartite" package was used to create a bipartite graph visualizing pollination networks, as well as calculate various quantitative species-level and network-level indices (Dormann et al., 2023). The following species-level statistics were calculated: degree, closeness centrality, and betweenness centrality. Degree is the number of partner species a given species has. Degree distributions are usually heavily skewed in mutualistic networks, with many low-degree species in both trophic levels (Valdovinos et al., 2009). Closeness centrality (CC) describes the proximity in the model of a given species to others in the same trophic level. Where n is the total number of species and d_{ij} is the shortest path between species i and j, CC of species i is given as:

$$CC_i = \sum_{j=1;i\neq j}^{n} \frac{d_{ij}}{n-1}$$

Betweenness centrality (BC) describes how important a species is in connecting other species to the network through shared pollinator interaction. Where n is the number of species in a network, g_{jk} is the number of shortest paths between any two species, and $g_{jk}(i)$ is the number of paths within g_{jk} that pass through species i, BC of species i is given as:

$$BC_i = 2\sum_{j<k;i\neq j} \frac{g_{jk}(i)/g_{jk}}{(n-1)(n-2)}$$

Nodes with high CC values can have profound effects on other nodes in the network, while nodes with high BC values help to connect otherwise isolated node pairs or modules to the rest of the network (Martín González et al., 2010).

Network-level statistics included connectance, specialization, nestedness, and robustness. Connectance is the extent to which the number of interactions in a pollinator network matches the potential number of interactions. This index is calculated by dividing the number of realized links by the total species richness, or plant richness multiplied by pollinator richness (Vizentin-Bugoni et al., 2018). Nestedness can be thought of as a network-scale extrapolation of degree. A nested network is one where, for example, specialist pollinators tend to interact with a subset of the plants that generalist pollinators interact with (Staniczenko et al., 2013). In this study, NODF or "Nestedness metric based on overlap and decreasing fill" was used to measure nestedness, with higher values indicating a more nested network. Specialization was quantified with the H2' index, or network-level standardized two-dimensional entropy. H2' values measure to what extent interactions in the network differ from an expected probability distribution (Blüthgen et al., 2007). Higher H2' values indicate higher specialization between plants and pollinators in the network. This index is derived from two-dimensional Shannon entropy, which quantitively measures specialization in the network. The word "quantitively" implies that interaction frequency between species pairs is incorporated into calculations, diferentiating this index from connectance, which only considers the presence/absence of interactions (Blüthgen et al., 2006). To create a standardized index between 0 and 1, Shannon entropy is constrained by its theoretical minimum and maximum values to calculate H2'. Where $H2$ is two-dimensional Shannon entropy for the network, $H2_{max}$ is the theoretical maximum value of $H2$, and $H2_{min}$ is the theoretical minimum value of $H2$, H2' is given as:

$$H_2' = \frac{H_{2max} - H_2}{H_{2max} - H_{2min}}$$

Finally, robustness is a measure of the resilience of one trophic level to extinctions in the other trophic level. This metric is based on the concept that, for example, extinctions of certain pollinators in a network will lead to secondary extinctions of plants that depend on those pollinators. Following the formula created by Burgos et al. (2007), robustness is the area under a secondary extinction curve calculated using network data. Ranging from 0 to 1, as robustness decreases for trophic level A, the effect of extinctions in trophic level B on trophic level A increases.

Additional statistical analyses were conducted to explore the study's three sub-questions. A Pearson Correlation Coefficient was calculated to find associations between pollinator robustness and various explanatory variables per network ($p \leq 0.05$). All species-level indices were found to be not normally distributed, so non-parametric statistics were used to analyze these values. A Mann-Whitney U test was used to test for a statistically significant difference in degree between non-native and native plants across all three networks ($p \leq 0.05$). To find key pollinator species, values for degree, betweenness centrality, and closeness centrality were processed in a Principal Component Analysis (PCA) following Sazima et al. (2010). A PCA was used due to the high correlation ($p \leq 0.05$) between the three explanatory variables and was calculated using the "psych" R package (Revelle, 2024). The first component of the PCA became a centrality index used to assess the importance of each pollinator to its respective network (Crespo Ampudia et al., 2021). The two species with the most positive centrality values in each habitat were chosen as key species, while all species with negative values were considered peripheral species.

Ethics Statement

This study did not include human subjects. As transects were often placed on private property, informed consent of all property owners was obtained before sampling at each site. This included explaining the project and the low-impact nature of its sampling methods. The author speaks conversational Spanish, allowing for clear communication with local people throughout the project timeline. A presentation was given to members of the Villaflora community explaining the basic findings of the study and implications for conservation and land management. This report was also sent to staff at Fundación EcoMinga, with the intent of building upon the base of ecological knowledge near their reserve. In addition, steps were taken to minimize harm to all collected insects, including gentle handling and non-lethal freezing to allow for live release following identification. Plants were also not disturbed during sampling, as most transects included a defoliated area or path on which to walk.

Results

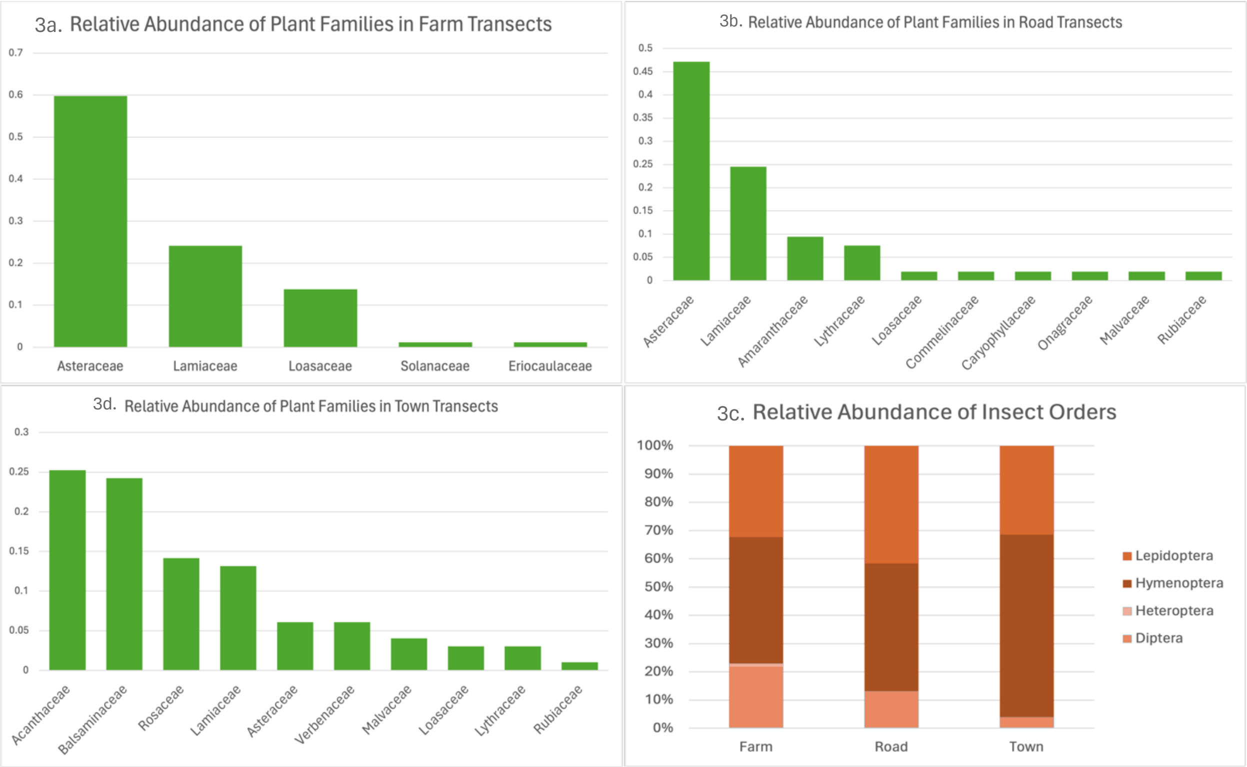
Diversity

239 plant-pollinator interactions were observed across the three networks, with 103 unique interactions between 30 plant species and 72 insect species. Full species lists for each network can be found in Appendix A. Individual transects and agglomerated networks varied considerably in terms of species composition and network characteristics (see Table 1). 87 interactions were observed in the "farm" network, compared with 99 in the town network, and 53 in the road network. Plant richness was highest in the road network, while pollinator richness was highest in the "farm" network. "Farm" and "road" networks had similar percentages of native plants, while the town network had considerably less. Weedy herbs represented an overwhelming majority of plants across all sites.

	Plant Richness	% Native Plants	Pollinator Richness	Connectance	NODF	H2'	Pollinator Robustness
Farm	11	67	33	0.118	11.945	0.655	0.679
Town	15	30	29	0.083	6.301	0.890	0.587
Road	17	66	28	0.067	2.789	0.761	0.556

Table 1. Summary table for network characteristics across "farm," "town," and "road" networks. See Methods section for explanations of network-level statistics calculated with "bipartite."

Relative abundance of plant families was heavily skewed in all networks, with Asteraceae and Lamiaceae dominating in farms and roads (see Figures 3a and 3b). Acanthaceae and Balsaminaceae were the most abundant families in the "town" network (See Figure 3c). Hymenoptera was the most abundant insect family in all sites, followed by Lepidoptera and Diptera (See Figure 3d). One Heteropteran was found in a "farm" transect, *Paraheraeus sp.,* a type of seed bug. This individual was included in the study due to observed pollen transfer between *Jaegeria hirta* inflorescences. No hummingbirds, bats, or beetle pollinators were found.



Clockwise from top left: **Figure 3a.** Relative abundance of plant families in "farm"transects; **Figure 3b.** Relative abundance of plant families in road transects; **Figure 3c.** Relative abundance of insects orders across all three habitat types; **Figure 3d.** Relative abundance of plant families in town transects.

Rarefaction-based extrapolations indicated richness increases in all habitats with more sampling effort, especially for pollinators in agricultural transects and plants in community transects. Pairwise beta diversity was low between habitats, as seen in Table 2. Interestingly, while plant communities overlapped more than 40% between "town" and "road" transects and between "road" and "farm" transects, the overlap between "farm" and "town" transects was much lower.

	Farm-Town	Town-Road	Road-Farm
Pollinator *β*	25.81%	24.56%	16.39%
Plant *β*	23.08%	43.75%	42.86%

Table 2: Beta diversity (*β*) across pollination networks, expressed as Sørensen-Dice similarity. Percentages indicate the degree of species overlap for each trophic level.

Network Analysis

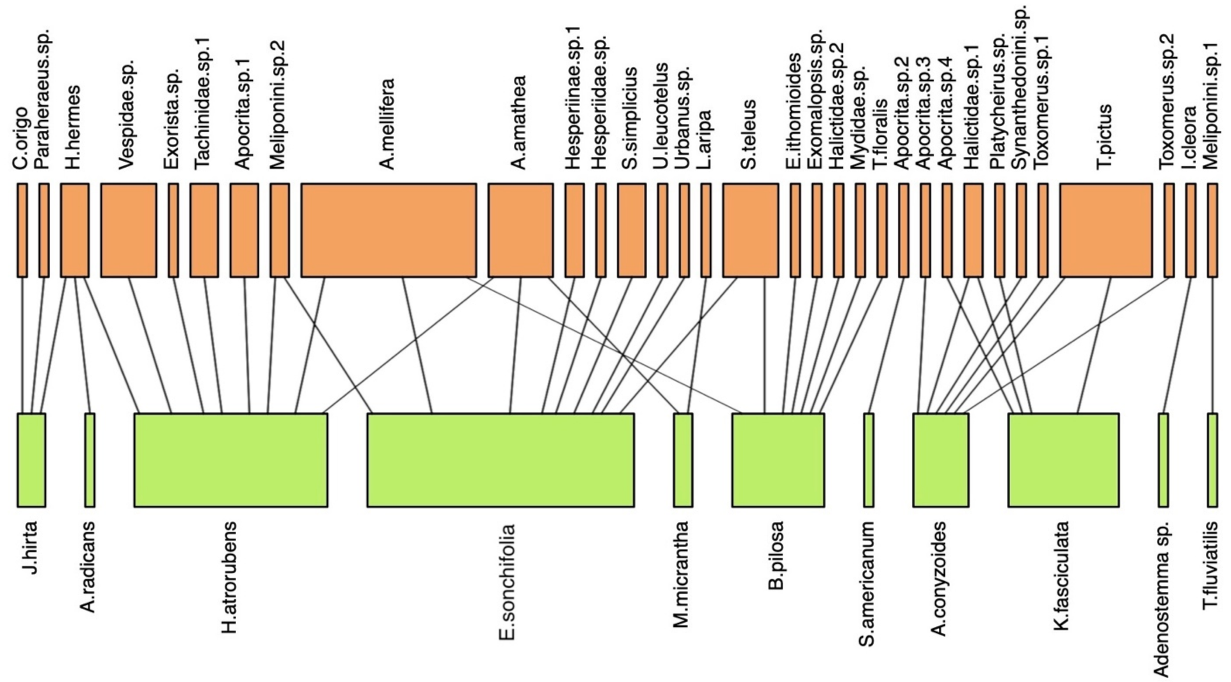


Figure 4a: Bipartite graph for "farm" transects. Green bars represent plants and orange bars represent pollinators. Lines represent observed interactions between species. Bar size represents the number of interactions including each species.

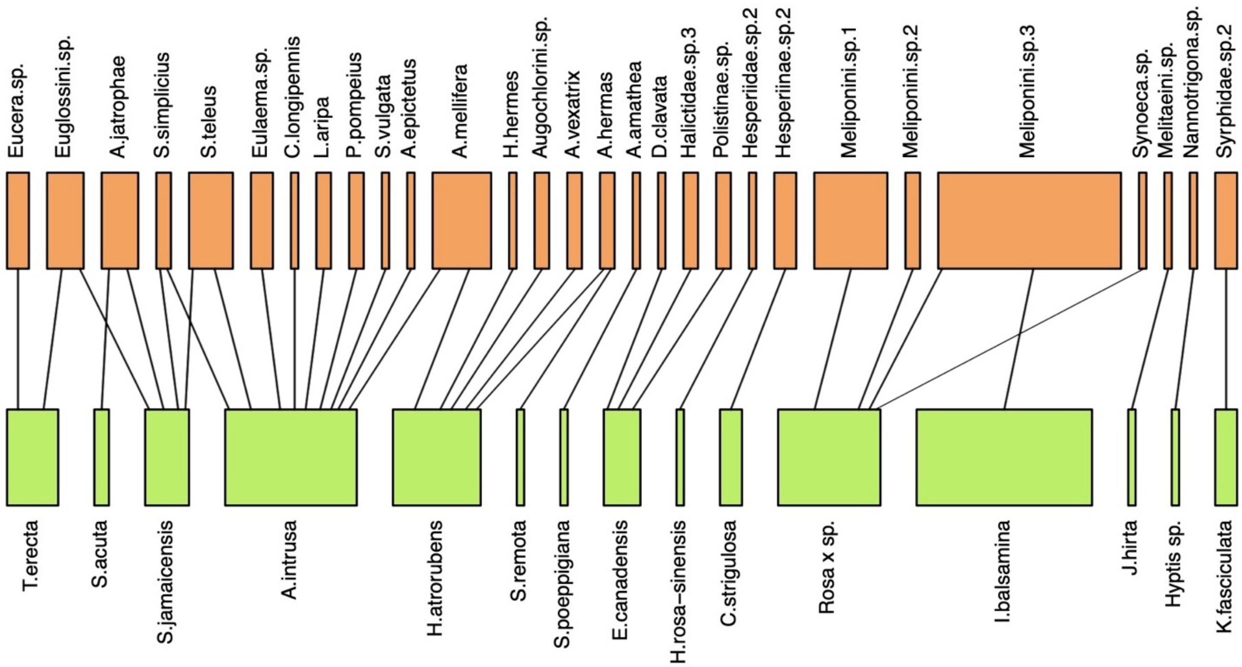


Figure 4b: Bipartite graph for "town" transects. Green bars represent plants and orange bars represent pollinators. Lines represent observed interactions between species. Bar size represents the number of interactions including each species.

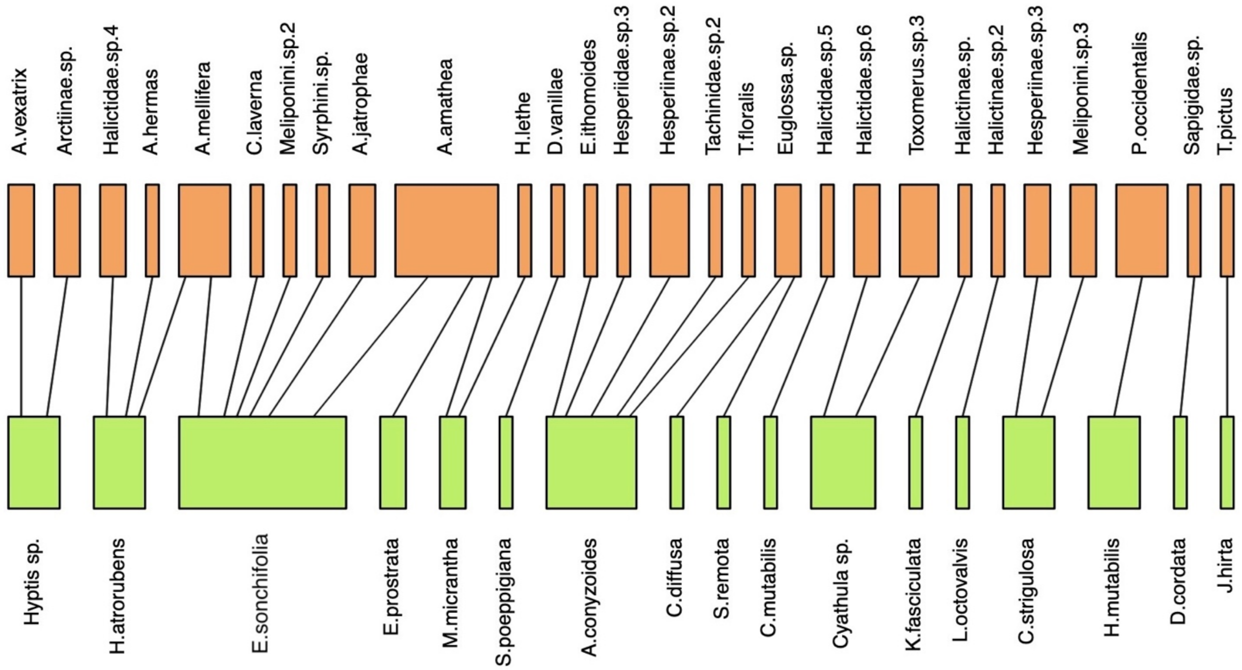


Figure 4c: Bipartite graph for “road” transects. Green bars represent plants and orange bars represent pollinators. Lines represent observed interactions between species. Bar size represents the number of interactions including each species.

As seen in Table 1, connectance was low across all networks, with the “road” habitat being the least connected. “Farm” was the most nested network, followed by “town” and “road.” H2’ specialization varied considerably, ranging from 0.66 in the “farm” network to 0.89 in the “town” network. This means the “town” network is almost entirely specialized. In general, pollinators in all networks were more robust to plant extinctions than plants were to pollinator extinctions. Pollinator robustness was highest in the “farm” network, which had the highest pollinator richness. Plant robustness was highest in the “road” network, which had the highest plant richness. Pearson correlation coefficient analysis indicated a positive correlation between pollinator robustness and pollinator richness (PCC=0.998; p=0.04), and a negative correlation between pollinator robustness and plant richness (PCC=-0.996; p=0.05). Nonsignificant correlations were found between pollinator robustness and both nestedness and proportion of native plants.

The Mann-Whitney *U* test revealed a significant increase in degree for non-native plants across all networks (p=0.03). The PCA analysis revealed a centrality dominance of the European honeybee, *Apis mellifera* across all plots. *A. mellifera* had a centrality index score of 3.46 in the “farm” network, 3.02 in the “town” network, and 3.36 in the “road” network. Another species of significance was *Anartia amathea*, with a centrality index of 3.38 in the “road” network and 2.33 in the “farm” network. The majority of species in each plot had negative centrality index values and were therefore considered peripheral. Full centrality index tables can be found in Appendix B. *A. mellifera* only visited flowers also visited by other pollinators, while *A. amathea* monopolized pollination of *Sida poeppigiana* in the “town” network and of *Eclipta prostrata* in the “road” network.

Discussion

This study compared pollination network composition and structure across 3 distinct types of disturbed habitat. In general, network characteristics aligned with previous literature on pollination networks in human-modified habitats. Many pollinator network studies show higher pollinator richness compared to plant richness (Gay et al., 2024; López-Ruiz, 2023; Diaz, 2023). The high diversity of the "road" network could be due to vehicle-mediated seed dispersal, as motorcycles and trucks passing by can easily introduce exotic seeds adhered to tires and disperse local seeds through wind draft (von der Lippe et al., 2013). This is corroborated by beta diversity values, which place the "road" network as a plant composition intermediary between the "town" and "farm" transects, showing higher plant species overlap with these habitats than either has with each other. Nevertheless, native weedy herbs of the families Asteraceae and Lamiaceae dominated in both the "farm" and "road" habitats. Pollinator richness has been shown to decrease with habitat size (Xiao et al., 2016). Due to the highly fragmented topography of roads, with thin strips of vegetation separated by several meters of barren roadway, low pollinator richness in the "road" network is expected. Following the results of previous studies, "farm" transects, which were either in or adjacent to agricultural areas, had the highest pollinator species richness (Jauker et al., 2009). This is likely due to higher floral abundance in agricultural areas, even though richness was not as high. Rarefaction results reveal incomplete sampling of both plants and pollinators, especially in habitats with comparatively low richness. This was likely due to concentrated sampling within a seasonal period, which limits which plants are in bloom, as well as cloudy weather conditions on many sampling days, which decreases pollinator abundance (Grange et al., 2021). The lack of hummingbird and bat encounters was due to a lack of flowers preferred by these animals.

The sharp decrease in native plant contribution to species richness in the "town" network is due to the presence of exotic ornamental plants, largely *Thunbergia erecta*, which originated in West Africa, and *Impatiens balsamina,* which originated in Asia. These species also contribute to the dominance of Acanthaceae and Balsaminaceae in the "town" network. Previous studies have indicated that non-native plants can offer more abundant nectar and pollen reward for pollinators (Bjerknes et al., 2007). This causes alien plants to attract a more diverse set of animal pollinators, making them more generalist than their native counterparts (Bartomeus et al., 2008). This phenomenon supports the significant increase in degree for non-native plants compared to natives across the three habitats. When extrapolated to a landscape scale, these high-reward exotics can increase pollinator density and diversity within and across habitats, but at the expense of native plants (Bjerknes et al., 2007). Nevertheless, higher pollinator richness in the "farm" network compared to the "town" network may indicate that habitat continuity and floral density have a greater impact on pollinator richness than the severity of exotic plant invasion, although more research is needed on this subject.

Network-level statistics are powerful tools for comparing mutualistic networks, but indexes must be understood in their respective contexts. It is important to note that the value of connectance as a comparative statistic is limited by its negative association with network size (Valdovinos et al., 2009). For this reason, network connectance is best understood when compared to H2' specialization, which is impartial to network size (Blüthgen et al., 2006). Pollination networks in tropical areas often show low connectance and high network specialization, due to coevolution and/or spatiotemporal mismatching that prevents pollinators from accessing certain plants (Young et al., 2021). Similarly, all networks were relatively poorly connected and highly specialized, a result that is evident in the bipartite graphs (Figures 4a-4c).

While these results are typical of tropical forests, they contradict the popular belief that altered habitats support less specialization between plants and pollinators (Xiao et al., 2016; Ashworth et al., 2004). Since altered habitats are more homogenous and less diverse, fewer resources are available for pollinators, which allows generalists to outcompete specialists or can force specialists to feed on a wider array of plant species (Pardee et al., 2023). However, a study by Vanbergen et al. (2017) in Scottish birch woodlands found disproportionally low connectance and high specialization in disturbed sites, compared to undisturbed. Another study found no significant connection between network specialization and land use intensity in a temperate grassland ecosystem (Weiner et al., 2014). Future studies could investigate such a potential relationship in low elevation tropical cloud forests and adjacent human-modified habitats.

Variation in nestedness (NODF) between the networks can be easily seen in the bipartite graphs (Figures 4a-4c). The "farm" network had the most generalist plants, which allowed a nested structure to form. Since nestedness is essentially redundancy of plant-pollinator interactions within the network, it's unsurprising that the most nested networks were also the most connected. However, no correlation has been proven between nestedness and environmental quality (Soares et al., 2017). Therefore, variation in nestedness across the three networks is more likely a byproduct of structural factors such as heterogeneity in species degree or specific plant morphologies (Mariani et al., 2019; Johnson et al., 2013).

Pollinator robustness is a useful measure of the resilience of a pollinator community to disturbance. Networks that are more robust are able to support pollinators, and likewise the plants they visit, even if land use changes continue to alter the architecture of the network. However, networks that lack robustness can experience extinction cascades of plants and pollinators that lead to community collapse (Bascompte & Scheffer, 2023). In a study comparing pollination networks across a gradient of urbanization, Udy et al. (2020) also found higher robustness in agricultural plots, followed by villages. "Farm" and "town" networks might show increased robustness due to more controlled land management, although the processes connecting management intensity and robustness remain a subject of debate (Proesmans et al., 2024). Previous systematic reviews have established that various structural network characteristics mediate and affect robustness (Huang et al., 2021; James et al., 2012; Memmott et al., 2004). In this study, the only statistically significant correlations were between robustness and species richness for both plants and pollinators, indicating a lack of sufficient variation in other explanatory variables across the habitats. Correlations between pollinator robustness and species richness tend to be positive for both plants and pollinators since diverse communities are generally more resilient to disturbance, thereby reducing the risk of extinction cascades (Huang et al., 2021). Pollinator richness followed this pattern when compared with robustness, but plant richness revealed a negative correlation. This could be due to the conflicting influence of plant richness and nestedness, since nestedness decreased as plant richness increased. Nestedness showed a strong positive correlation with pollinator robustness across the networks, although this correlation was not significant ($p>0.05$). However, since p-values are affected by sample size, a larger-scale study might show a significant correlation between these variables, as other literature has shown (Gómez-de-Mariscal et al., 2021; Mariani et al., 2019). Interestingly, there was no significant correlation between pollinator richness and percent of native plants in each network. This is because the "farm" and "road" networks had quite distinct robustness values but nearly identical native plant percentages. This result suggests that that other variables have a greater effect on robustness in disturbed habitats than native plant abundance. It is therefore necessary to create a niche continuity plan when conducting invasive plant removal in disturbed habitats, as some alien plants might be important contributors to pollinator success and network stability.

This means selecting native plants that share a pollinator niche with invasive plants, therefore rewiring the network to preserve robustness (Bascompte & Scheffer, 2023).

The centrality index analysis was conducted to uncover keystone pollinators in the three networks that are vital to ecosystem functioning (Martín González et al., 2010). Identifying the species with outsized contributions to network structure can inform conservation/restoration actions, placing priority on either the species themselves or the relationships they have with plants (Crespo Ampudia et al., 2021). Like in these networks, most mutualistic assemblages consist of many peripheral species and a few key species (Sazima et al., 2010). The two most central pollinator species across all networks, *Apis mellifera* and *Anartia amathea*, were also two of the most generalist, as seen in Figures 4a-4c. It's logical that the pollinators that connect the most nodes to the rest of the network would also be highly generalist. *Apis mellifera* is an introduced species of bee, originating in Europe. In other parts of Ecuador and much of the world, feral honeybees have begun to compete with and/or replace the pollination services of native bees on certain plants (Crafford, 2020). As noted earlier, all plants visited by *A. mellifera* were also visited by native pollinators, indicating intra-pollinator competition for nectar and pollen resources. This poses a direct threat to the survival of native pollinators, and potentially to plants as well, since the relative effectiveness of *A. mellifera* pollination for tropical plants is not well understood (Knowlton et al., 2022). *Anartia amathea,* on the other hand, is one of the most common native butterflies in the neotropics (Silberglied et al., 1979). PCA results reveal that *A. amathea* is a significant contributor to the structure of pollination networks across the three habitats, especially in the "road" network. For this reason, the plants visited most commonly by this butterfly should be avoided when land managers conduct vegetation removal. However, this analysis overlooked many specialist, peripheral pollinators that provide vital pollination services for certain plants, thereby boosting local biodiversity. Conservation efforts therefore must be holistic, protecting the most central relationships within the network, while also preserving the wider native pollinator community.

These results indicate that while pollination networks differ considerably among land use types in the Chocó, more research is needed to uncover the mechanisms of structural and functional change in these networks over time. Future studies comparing the presented data with networks in conserved cloud forest would further elucidate how human-managed habitats could be improved for pollinators while simultaneously producing benefits for humans. In addition, long-term experimental studies could develop restoration regimes that retain or improve network robustness and boost pollinator diversity. While conserving pollinator species is important for local biodiversity, reforming land management techniques to enhance pollinator habitat in human-altered areas has numerous secondary benefits that could support a local agricultural and ecotourism-based economy.

Conclusion and Recommendations

This study built upon previously tested statistical techniques to understand the effects of biodiversity variation and alien plant invasions on pollinator networks in an understudied and threatened landscape. Although specific network characteristics varied across the three habitats in this study, all networks shared characteristics of disturbed habitats. As a region dependent on animal-pollinated crops and bordering primary cloud forest, the Río Manduriacu valley is a prime location for pollinator habitat restoration. Agricultural areas adjacent to forest, including secondary or disrupted forest, can benefit from the services of pollinators adapted to the transition zone (Krishnan, 2020). In the case of Villaflora, upland forest fragments should be conserved as to preserve habitat for native Meliponine bees that pollinate pitahaya and plantain crops. In addition, native flowers should be preserved and planted in agricultural areas to support these same edge-zone pollinators, thereby facilitating pollinator network activity and robustness in the forest as well (Buhk et al., 2018; McDonald et al., 2009). Native flowers should also be prioritized in gardens, as they will not only support native pollinators, but can additionally fortify pollination networks in nearby farms (Langellotto et al., 2018). By supporting native plants and native pollinators, the dominance of invasive pollinators such as *Apis mellifera* will be reduced. A diverse community of native flowers also boosts soil health and stability, and adds to the aesthetic beauty of a region (Wratten et al., 2012). Finally, flowering plants along roads should not be removed, as to support pollinator corridors between habitat fragments (Dietzel et al., 2023). In order to predict the effects of these restoration projects on network stability, future studies could investigate the robustness outcomes of replacing exotic plants with native plants in disrupted habitats, as well as the relative effectiveness of *Apis Mellifera* as a pollinator in this area. Pollination ecology is still a relatively new field of study, and given the localized nature of plant-pollinator mutualisms, there exists great potential for applied research that can help reverse pollinator declines on a global scale.

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Appendix A

Full plant and pollinator species list for "farm," "town," and "road" networks.

Plant Family	Plant Species	Growth habit	Native?
Asteraceae	Acmella radicans	Herb	Yes
Asteraceae	Adenostemma sp.	Herb	Yes
Asteraceae	Ageratum conyzoides	Herb	Yes
Asteraceae	Bidens pilosa	Herb	Yes
Asteraceae	Emilia sonchifolia	Herb	No
Lamiaceae	Hyptis atrorubens	Herb	Yes
Asteraceae	Jaegeria hirta	Herb	Yes
Loasaceae	Klaprothia fasciculata	Herb	Yes
Asteraceae	Mikania micrantha	Vine	Yes
Solanaceae	Solanum americanum	Herb	Yes
Eriocaulaceae	Tonina fluviatilis	Herb	Yes

Table A1. Plant species encountered in agricultural transects, representing the plant community for the "farm" network.

Plant Family	Plant Species	Growth habit	Native?
Acanthaceae	Asystasia intrusa	Herb	No
Lythraceae	Cuphea strigulosa	Herb	Yes
Asteraceae	Erigeron canadensis	Herb	No
Malvaceae	Hibiscus rosa-sinensis	Herb	No
Lamiaceae	Hyptis atrorubens	Herb	Yes
Lamiaceae	Hyptis sp.	Herb	Yes
Balsaminaceae	Impatiens balsamina	Herb	No
Asteraceae	Jaegeria hirta	Herb	Yes
Loasaceae	Klaprothia fasciculata	Herb	Yes
Rosaceae	Rosa x sp.	Shrub	No
Malvaceae	Sida acuta	Undershrub	Yes
Malvaceae	Sida poeppigiana	Undershrub	Yes
Rubiaceae	Spermacoce remota	Herb	Yes
Verbenaceae	Stachytarpheta jamaicensis	Herb	Yes
Acanthaceae	Thunbergia erecta	Shrub	No

Table A2. Plant species encountered in populated transects, representing the plant community for the "town" network.

Plant Family	Plant Species	Growth habit	Native?
Asteraceae	Ageratum conyzoides	Herb	Yes
Lamiaceae	Cantinoa mutabilis	Herb	Yes
Commelinaceae	Commelina diffusa	Herb	Yes
Lythraceae	Cuphea strigulosa	Herb	Yes
Amaranthaceae	Cyathula sp.	Herb	No
Caryophyllaceae	Drymaria cordata	Herb	Yes
Asteraceae	Eclipta prostrata	Herb	Yes
Asteraceae	Emilia sonchifolia	Herb	No
Lamiaceae	Hyptis atrorubens	Herb	Yes
Lamiaceae	Hyptis mutabilis	Herb	Yes
Lamiaceae	Hyptis sp.	Herb	Yes
Asteraceae	Jaegeria hirta	Herb	Yes
Loasaceae	Klaprothia fasciculata	Herb	Yes
Onagraceae	Ludwigia octovalvis	Herb	Yes
Asteraceae	Mikania micrantha	Vine	Yes
Malvaceae	Sida poeppigiana	Undershrub	Yes
Rubiaceae	Spermacoce remota	Herb	Yes

Table A3. Plant species encountered in road transects, representing the plant community for the "road" network.

Insect Order	Insect Species
Lepidoptera	Anartia amathea
Hymenoptera	Apis mellifera
Hymenoptera	Apocrita sp. 1
Hymenoptera	Apocrita sp. 2
Hymenoptera	Apocrita sp. 3
Hymenoptera	Apocrita sp. 4
Lepidoptera	Calycopis origo
Lepidoptera	Eresia ithomioides
Hymenoptera	Exomalopsis sp.
Diptera	Exorista sp.
Hymenoptera	Halictidae sp. 1
Hymenoptera	Halictidae sp. 2
Lepidoptera	Hermeuptychia hermes
Lepidoptera	Hesperiidae sp.
Lepidoptera	Hesperiinae sp. 1
Lepidoptera	Ithomia cleora
Lepidoptera	Leptophobia aripa
Hymenoptera	Meliponini sp. 1
Hymenoptera	Meliponini sp. 2
Diptera	Mydidae sp.
Heteroptera	Paraheraeus sp.
Diptera	Platycheirus sp.
Lepidoptera	Spicauda simplicius
Lepidoptera	Spicauda teleus
Hymenoptera	Synanthedonini sp.
Diptera	Tachinidae sp. 1
Diptera	Toxomerus floralis
Diptera	Toxomerus pictus
Diptera	Toxomerus sp. 1
Diptera	Toxomerus sp. 2
Lepidoptera	Uranophora leucotelus
Lepidoptera	Urbanus sp.
Hymenoptera	Vespidae sp.

Table A4. Insect species encountered in agricultural transects, representing the pollinator community for the "farm" network.

Insect Order	Insect Species
Diptera	Adejeania vexatrix
Lepidoptera	Anartia amathea
Lepidoptera	Anartia jatrophae
Lepidoptera	Anthanassa hermas taeniata
Lepidoptera	Anthoptus epictetus
Hymenoptera	Apis mellifera
Hymenoptera	Augochlorini sp.
Lepidoptera	Cecropterus longipennis
Diptera	Dioprosopa clavata
Hymenoptera	Eucera sp.
Hymenoptera	Euglossini sp.
Hymenoptera	Eulaema sp.
Hymenoptera	Halictidae sp. 3
Lepidoptera	Hermeuptychia hermes
Lepidoptera	Hesperiidae sp. 2
Lepidoptera	Hesperiinae sp. 2
Lepidoptera	Leptophobia aripa
Hymenoptera	Meliponini sp. 1
Hymenoptera	Meliponini sp. 2
Hymenoptera	Meliponini sp. 3
Lepidoptera	Melitaeini sp.
Hymenoptera	Nannotrigona sp.
Hymenoptera	Polistinae sp.
Lepidoptera	Pompeius pompeius
Lepidoptera	Spicauda simplicius
Lepidoptera	Spicauda teleus
Lepidoptera	Staphylus vulgata
Hymenoptera	Synoeca sp.
Diptera	Syrphidae sp. 2

Table A5. Insect species encountered in populated transects, representing the pollinator community for the “town” network.

Insect Order	Insect Species
Diptera	Adejeania vexatrix
Lepidoptera	Anartia amathea
Lepidoptera	Anartia jatrophae
Lepidoptera	Anthanassa hermas taeniata
Hymenoptera	Apis mellifera
Lepidoptera	Arctiinae sp.
Lepidoptera	Calephelis laverna
Lepidoptera	Dione vanillae
Lepidoptera	Eresia ithomoides
Hymenoptera	Euglossa sp.
Hymenoptera	Halictidae sp. 4
Hymenoptera	Halictidae sp. 5
Hymenoptera	Halictidae sp. 6
Hymenoptera	Halictinae sp.
Hymenoptera	Halictinae sp. 2
Lepidoptera	Hesperiidae sp. 3
Lepidoptera	Hesperiinae sp. 2
Lepidoptera	Hesperiinae sp. 3
Lepidoptera	Hypanartia lethe
Hymenoptera	Meliponini sp. 2
Hymenoptera	Meliponini sp. 3
Hymenoptera	Polybia occidentalis
Hymenoptera	Sapigidae sp.
Diptera	Syrphini sp.
Diptera	Tachinidae sp. 2
Diptera	Toxomerus floralis
Diptera	Toxomerus pictus
Diptera	Toxomerus sp. 3

Table A6. Insect species encountered in road transects, representing the pollinator community for the “road” network.

Appendix B

Centrality index values for pollinators in "farm," "town," and "road" habitats

Name	Centrality Index
Apis mellifera	3.460
Anartia amathea	2.332
Halictidae sp. 1	2.300
Spicauda teleus	1.224
Meliponini sp. 2	1.070
Halictidae sp. 2	0.192
Toxomerus floralis	0.192
Hesperiidae sp.	-0.156
Hesperiinae sp. 1	-0.156
Spicauda simplicius	-0.156
Uranophora leucotelus	-0.156
Urbanus sp.	-0.156
Apocrita sp. 1	-0.166
Exorista sp.	-0.166
Toxomerus pictus	-0.166
Vespidae sp.	-0.166
Eresia ithomioides	-0.225
Exomalopsis sp.	-0.225
Hermeuptychia hermes	-0.225
Mydidae sp.	-0.225
Tachinidae sp. 1	-0.225
Leptophobia aripa	-0.412
Calycopis origo	-0.432
Paraheraeus sp.	-0.432
Apocrita sp. 3	-0.638
Synanthedonini sp.	-0.638
Toxomerus sp. 1	-0.638
Toxomerus sp. 2	-0.638
Apocrita sp. 4	-0.697
Platycheirus sp.	-0.697
Apocrita sp. 2	-0.992
Ithomia cleora	-0.992
Meliponini sp. 1	-0.992

Table B1. Pollinator species and their centrality scores in the "farm" habitat. Species with a positive centrality index score are considered key to network ecology, while those with negative scores are considered peripheral.

Name	Centrality Index
Apis mellifera	3.205
Spicauda simplicius	1.845
Spicauda teleus	1.845
Euglossini sp.	1.446
Anthanassa hermas taeniata	0.792
Anartia jatrophae	0.748
Meliponini sp. 3	0.340
Anthoptus epictetus	0.001
Cecropterus longipennis	0.001
Eulaema sp.	0.001
Leptophobia aripa	0.001
Polistinae sp.	0.001
Staphylus vulgata	0.001
Adejeania vexatrix	-0.184
Augochlorini sp.	-0.184
Hermeuptychia hermes	-0.184
Eucera sp.	-0.420
Meliponini sp. 1	-0.637
Meliponini sp. 2	-0.637
Synoeca sp.	-0.637
Dioprosopa clavata	-0.714
Halictidae sp. 3	-0.714
Pompeius pompeius	-0.714
Anartia amathea	-0.867
Hesperiidae sp. 2	-0.867
Hesperiinae sp. 2	-0.867
Melitaeini sp.	-0.867
Nannotrigona sp.	-0.867
Syrphidae sp. 2	-0.867

Table B2. Pollinator species and their centrality scores in the "town" habitat. Species with a positive centrality index score are considered key to network ecology, while those with negative scores are considered peripheral.

Name	Centrality Index
Anartia amathea	3.376
Apis mellifera	3.363
Euglossa sp.	0.345
Anartia jatrophae	0.189
Calephelis laverna	0.189
Meliponini sp. 2	0.189
Syrphini sp.	0.189
Anthanassa hermas taeniata	-0.015
Halictidae sp. 4	-0.015
Hypanartia lethe	-0.096
Eresia ithomoides	-0.117
Hesperiidae sp. 3	-0.117
Hesperiinae sp. 2	-0.117
Toxomerus floralis	-0.117
Tachinidae sp. 2	-0.117
Adejeania vexatrix	-0.483
Arctiinae sp.	-0.483
Halictidae sp. 6	-0.483
Hesperiinae sp. 3	-0.483
Meliponini sp. 3	-0.483
Toxomerus sp. 3	-0.483
Dione vanillae	-0.605
Halictidae sp. 5	-0.605
Halictinae sp.	-0.605
Halictinae sp. 2	-0.605
Polybia occidentalis	-0.605
Sapigidae sp.	-0.605
Toxomerus pictus	-0.605

Table B3. Pollinator species and their centrality scores in the "road" habitat. Species with a positive centrality index score are considered key to network ecology, while those with negative scores are considered peripheral.