Stability and resilience of plant-pollinator networks in an Andean montane community in southern Ecuador

Rachel Crafford

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Advisor: Dr. Jessie Knowlton

Co-authors: Francesca Sajedi, Dr. Erin Wilson-Rankin, Dr. Boris Tinoco
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Abstract

Mutualistic interactions sustain biodiversity and influence community stability. If there are only a few interactions within a community, or multiple interactions that are weak, the community is more likely to collapse. This research investigated the stability of a plant-pollinator community in the Ecuadorian Andes to understand how vulnerable these interactions are to environmental stressors such as climate change and habitat degradation. To do this, we used two species interaction networks based on foraging fidelity (i.e., consistent returns to a particular plant species) and floral association data from both native and non-native pollinators. We used the network metrics connectance, specialization, and weighted network nestedness to determine the strength of these interactions, and therefore, the resiliency of this montane community. Based on these metrics, we found that our visitation network is relatively robust to ecosystem stressors, however, our larger-scale survey, which may be a more accurate depiction of the community due to sample size and increased diversity, showed a lack of resilience to stressors. Honey bees (Apis mellifera) were much more abundant than native bees in both networks, and may be providing many of the pollination services previously provided by native bees. Honey bees were generalists at the species level, but individuals were faithful to particular plant species. This research can help inform future conservation and non-native species management efforts, and can be used to further understand the nuanced relationships between plants and pollinators, which are essential to agricultural production and ecosystem maintenance on a global scale.
Introduction

Mutualistic interactions between species help to sustain biodiversity and community stability, especially when these species are highly connected (Thebault & Fontaine 2010). If there are only a few interactions within a community, or many interactions that are weak, the ecosystem is more likely to collapse (Thebault & Fontaine 2010). This interconnectivity can facilitate species coexistence (Bastolla et al. 2009), enhance ecosystem flexibility to environmental disturbance (Okuyama & Holland 2008), and maximize total abundance of species in the ecosystem (Suweis et al. 2013). In highly connected communities, there is often functional redundancy as well, where similar functional roles are carried out by multiple different species (Rosenfeld 2002). This overlap of functional roles within highly connected communities also contributes to overall resilience by ensuring that key services are maintained within a larger ecosystem (Rosenfeld 2002). By studying these networks of interactions between species, we gain a better idea of community and ecosystem tolerances to disturbance, since the threshold at which a community will collapse may depend upon the strength of these mutualistic interactions (Fortuna & Bascompte 2006). Community response to stressors such as habitat fragmentation, habitat loss, and global climate change is affected by the structure of the interaction networks that occur within the community (Fortuna & Bascompte 2006). Thus, it is necessary to assess these critically important and complex networks of species interactions.

The mutualistic relationship between plants and their pollinators is one example of a fundamental network of interactions among species in an ecosystem. Within the last decade research has ramped up in an effort to better understand the increased negative impacts of anthropogenic stressors on bee pollinators, such as pesticide use, disease, habitat loss and lack of flowers (Goulson et al. 2015), invasive species (Stout & Morales 2009) and climate change
Finally, it is well known that mountainous environments are among those that are most affected and at risk from climate change (Cárdenas & Mishra 2017; Fort 2015; Beniston 2005); their extreme climatic conditions, short growing seasons, steep slopes, and shallow ground place them among the most fragile of ecosystems (Santamaria et al. 2014). Thus, these high elevation regions could rely strongly on mutualistic interactions, which would allow the community to be more flexible and resistant to disturbance. However, when the mutualistic community dynamics themselves, such as the plant-pollinator interactions, are also threatened by multiple stressors (invasive species, climate change), it is difficult to predict how reliable these mutualistic dynamics may be in maintaining overall resistance and wellbeing of montane communities.

As introduced and invasive species continue to spread beyond their native ranges, much attention has been paid to their negative effects on maintenance of biodiversity. Some large-scale effects include overall homogenization of biota as species richness, evenness, and diversity are reduced due to introduced species outcompeting native species (Hejda et al. 2009). Because bees are important pollinators in many different ecosystems (Klein et al. 2007; Levin 1983), various species have been introduced to countries outside of their range. Introduced European honey bees (Apis mellifera) are able to thrive in environments where they are not native due to their generalist foraging habits, which have enabled them to adapt to and colonize many habitats worldwide (Waser & Ollerton 2006). Honey bees also show highly social behavior, remain active longer than the blooming period of most plant species, and are able to nest in colonies consisting of thousands of individuals, which also helps them become and stay established in new habitats (Waser & Ollerton 2006).
Conversely, native pollinators are usually solitary, short lived, and more specialized than honey bees in their foraging habits, because in many cases their foraging activity can take place within a single plant species’ flowering period, meeting all of the needs of the pollinator (Waser & Ollerton 2006). To date, research has focused primarily on interspecific competition between native and introduced bees for floral resources, as well as the ability of honey bees to pollinate exotic weeds and disrupt pollination of native plants (Goulson 2003). Competition between these pollinators has been shown to hinder growth, survival, and reproduction for native species (Paini 2004), negatively affecting the plant-pollinator networks in various communities (Kato et al. 1999; Schaffer et al. 1983; Valido et al. 2019).

Climate change, another stressor to community wellbeing, has the potential to disrupt or eliminate mutualistic ecological interactions (Memmott et al. 2007) because of its effects on the phenology, local abundance, and large scale distribution of biota (Hegland et al., 2009). While phenological responses to climate change, such as flowering time of plants and subsequent appearance of pollinators, may occur parallel to one another as an adaptation to global rise in temperature, there might also be significant variation in these responses, leading to a mismatch in pollination interactions, and thus, disruption in the pollination network (Hegland et al. 2009). A change in local species abundance and distribution of those species across a habitat range, such as on the side of a mountain, could also lead to novel species combinations (Hegland et al. 2009).

As the effects of non-native species, habitat fragmentation, and climate change as stressors continue to be studied, it is important that they are considered in the context of one another since they are all key processes affecting global biodiversity and interspecific interactions (Walther et al. 2009). Therefore, this research focused on the following broad question: How stable is the plant-pollinator community in the high Andean montane scrub, and,
thus, how vulnerable are these interactions to impacts from ecosystem stressors such as climate change and habitat degradation? To determine the level of specialization of these interactions, and therefore, the level of resiliency of this montane community, we constructed species interaction networks based on data we collected on foraging fidelity (i.e., consistent returns to a particular plant species or area) (Cecala & Rankin 2020) of both native and non-native pollinators. Further, we tested several different hypotheses: 1) Introduced honey bees (Apis mellifera) will be more generalist than native bees in their foraging habits at the species level, 2) native bees will be more specialized and will exhibit higher levels of plant species fidelity than honey bees, and thus, 3) both the mark-recapture network and Hymenoptera floral association network will be resilient to environmental stressors based on high interconnectivity and nestedness facilitated by the generalist (honey bee) and specialist (native bee and wasp) pollinators that make up these networks (Menz et al. 2011; Thebault & Fontaine 2010). It is essential to know what role insect pollinators play in this larger web of mutualisms if we are to assess the vulnerability of this environment to further disturbance and plan conservation efforts accordingly.

METHODS

Study Site

This research was conducted in the southern Ecuadorian Andes at Universidad del Azuay’s El Gullán research station in the province of Azuay. El Gullán is located in the Andean community of La Paz, about 52 kilometers south of the city of Cuenca (3°20'17.35"S, 79°10'16.89"W). La Paz is in the canton of Nabon situated within the sub-basin of the Leon River. The property sits at 3,000-3,400 meters above sea level, encompasses 160 hectares, and was set aside by the university for various biology, ecology, and conservation projects. This site
is characterized by high-elevation montane shrubland vegetation dominated by several different *Baccharis* (Asteraceae) and *Puya* (Bromeliaceae) plant species, includes many flowering species, such as *Oreocallis grandiflora* (Proteaceae) and *Macleania rupestris* (Ericaceae), and has a seasonal rain pattern consisting of a wet period from September to May and a dry season from June to August (Cardenas et al. 2017). The study site is also home to species of endemic frogs, bees, orchids, birds, and mosses, although little is known about the biodiversity in this ecosystem. Finally, El Gullán and surrounding areas are highly fragmented due to cattle grazing, and are also threatened by climate change due to the high elevation of the area (Chacon-Vintimilla 2018).

**Study Design**

All data was collected between July 16th and July 31st of 2019. To census the plant-pollinator community at El Gullán, we set up four transects along pre-existing trails where we conducted plant surveys and pollinator mark-recapture to measure species fidelity. In addition, we also collected all of the bees and wasps that we found on each transect to get a better idea of the species composition of hymenopterans on the transects. From these specimens, we will be able to gather pollen samples to later identify which species of plants each pollinator was visiting via DNA barcoding (in collaboration with Dr. Wilson-Rankin at UC Riverside). Transect lines at El Gullán were located on the path “El Mirador.” The transects were each 100 m in length and separated from one another by at least 100 m. The transects were spaced in this way because bees, regardless of body size, generally do not extend their foraging ranges beyond 300 m, with the average distance between 100-255 m (Zurbuchen et al. 2010), therefore reducing the chances of recapturing a bee that had been marked on a transect other than the one where it was initially
marked. Pollinator capture and flower data were taken from ~2 meters on either side of the transects.

**Flower Species Selection & Identification**

I chose six different species of flowering plants on the transects from which to collect pollinators, in an effort to maintain consistency for mark-recapture by taking a sub-sample of the larger floral community (see Williams et al. 2001). The flowers that I chose were *Ageratina pseudochilca* (Asteraceae), *Dendrophorbium sp.* (Asteraceae), *Ageratina sp.* (Asteraceae), *Ilex sp.* (Aquifoliaceae), *Gaultheria reticulata* (Ericaceae), and *Miconia sp.* (Melastomataceae). I chose these flowers in particular because these were the most common species that I noticed bees visiting. Before any pollinators were caught, myself and a field technician walked each transect line and identified any flowering plants within two meters on either side of the trail. To identify the plant to species, we used a field guide put together by the Universidad del Azuay, which had a picture and the scientific name of the most common flowering plants at the research station. After identifying the plant species themselves, we counted the number of open flowers on the plants, because the total number of open flowers per plant species per transect allows for the estimation of plant species-specific resource abundance (Maglianesi et al. 2014). *A. pseudochilca* and *Dendrophorbium sp.* are composite flowers that produced a collection of florets which made up the inflorescence, so for these, we counted the number of florets individually within the head and extrapolated to get an estimate for the entire plant, as each one presented an opportunity for a pollinator to visit the plant. This count gave us an estimate of the total floral resource abundance in this community.
Hymenoptera Floral Association Study: Bees and Wasps

Once we collected data on which flowering plant species were present at the field site, we censused the pollinator community, focusing on bees and wasps (Hymenoptera) specifically as these are the most abundant at this location. At El Gullán, pollinator activity generally began at around 10:00 am and continued until 2:00 pm each day, which was determined based on observations made by the Entomology department at Universidad del Azuay during their own research projects. Activity was heightened when it was sunny, and we had the most success in catching Hymenopterans when there was little to no wind. Using insect nets, we collected all bees and wasps on each transect within this time window, for a total of four person-hours on each transect. Captured insects were transferred from the net to a small plastic tube for later identification and pollen collection at the lab. During collection, we numbered the tubes that we put each specimen in, taking note of which flower species we found them on (if any) to create an association network between the plants and pollinators.

Mark-recapture Study

For this experiment, we examined floral fidelity of honey bees and native bees using mark-recapture. In order to mark individual bees, we constructed a tool similar to a queen marking cage, which is a syringe-like tool. We used a hollow plastic tube with one opening covered by fine mesh, and a sponge with a chop-stick attached to serve as a plunger (Fig. 1a) (see Cecala & Rankin 2020; Yamamoto et al. 2014).

For two person-hours twice a day (once in the morning and once in the afternoon) between the hours of 10:00 am and 2:00 pm we walked each 100m transect line and collected all bees observed on the same 6 plant species as the wasp and bee survey described above. When we
caught a pollinator, it was transferred from the insect net and into the open end of the plastic tube. Once it was in the marking tube, the sponge plunger was inserted into the open end and pushed upwards to gently press the bee against the mesh, thorax side facing up (Fig. 1b). The thorax was then marked with a dot of color through the mesh with a paint marker. The color of the paint was specific to the species of flower where the bee was found foraging (Fig. 1c & d). We utilized six different colors of paint markers to correspond to the six species of flowers that I had pre-determined, and only marked bees found on those six species. If a bee was seen foraging on a flower species that was not one of those six species, it was not marked, but rather noted.

Recapture days took place the day after the pollinators were marked on each transect. We followed the same time schedule and procedure for recapturing the bees. When we found a pollinator that was already marked from the previous day, we marked it with a different color also corresponding to the flower that it was found on, so that we did not count it more than once. When we saw bees that were not marked, we noted which flowers they were seen on but did not catch them and mark them. Hymenopterans were collected from the transects either well before (at least six days) we conducted mark-recapture of pollinators on the same transect, or after mark-recapture was already complete so as not to affect the outcome of our mark-recapture efforts by collecting too many bees and wasps from the transects before the population could recover.
Figure 1: Images a and b show the marking cage tool that was used to mark bees that were caught; images c and d show two marked honey bees on *G. reticulata* and *A. pseudochilca* with their corresponding paint colors.

**Statistical Analyses.**

All analyses were conducted in R v. 3.5.1 (R Core Team, 2019) using RStudio. We used the package *bipartite* (Dormann et al. 2019) to assess key plant-pollinator network metrics for each transect in each study. For both studies, the mark-recapture and the Hymenoptera floral association study, we calculated connectance and weighted network nestedness using function 'networklevel', and species-level specialization (d’), using the function 'specieslevel' in package *bipartite* (Dormann et al. 2019). Each of these metrics follows a scale from 0 to 1, where a value of 0 indicates no connectance, nestedness, or specialization, and 1 suggests perfect connectance, perfect nestedness, and perfect specialization (Dormann et al. 2019). All three metrics serve as different ways of quantifying the strength of the interactions within the community to help predict its resilience to disturbance.
Network connectance, or the realized proportion of possible links (Dunne et al. 2002), is calculated by creating a proportion that represents all the possible interactions within a network compared to all of the interactions that actually occurred in that network (Dunne et al. 2002). We used connectance to measure how often species within the network interact with one another (Santamaria et al., 2014). If connectance is high in a plant-pollinator network, this indicates that each plant in the network is connected to multiple pollinators, which increases functional redundancy of pollinators and therefore strengthens network resilience to extinction (Memmott et al., 2004).

We also calculated weighted network nestedness, which shows the frequency of mutualistic partners with more generalized interactions compared to those partners with high specificity of interactions (Dormann et al. 2019; Valido et al. 2019). In a nested network, mutualistic partners with more generalized interactions appear more frequently than those with a higher specificity of interactions (Valido et al. 2019). When a network is nested, it means that the specialists in the network interact with a subset of the species that the generalists interact with. A nested system may be buffered against extinction, and therefore may indicate the stability of the community (Santamaria et al., 2014).

Finally, we utilized d’ as a measure of specialization at the species level for both the bees/wasps and the flowers censused during the Hymenoptera floral association and the mark-recapture studies. This metric calculates how much a species deviates from a random sampling of interacting partners (Dormann et al. 2019). It has been theorized that disturbance favors more generalist species for a variety of reasons; for example, specialists might have more restricted diet breadths and habitat or range requirements than generalists, making them more vulnerable to extinction (Vázquez & Simberloff 2002). Therefore, a measure of specialization tells us the
degree to which a species is vulnerable to extinction as a result of environmental stressors.

RESULTS

**Hymenoptera Floral Association Study**

Seventy-three specimens from four different families were collected from the hymenopteran census: Apidae (Figure 2a-e), Crabronidae (Figure 2f-g), Halictidae (Figure 2h-k), and Ichneumonidae (Figure 2l). These individuals were collected visiting eight different plant species: *Ageratina pseudochilca* (Asteraceae), *Baccharis obtusifolia* (Asteraceae), *Dendrophorbium sp.* (Asteraceae), *Gaultheria reticulata* (Ericaceae), *Ilex sp.* (Aquafoliaceae), *Miconia sp.* (Melastomateae), *Monnina pycnophylla* (Polygalaceae), and *Oreocallis grandiflora* (Proteaceae). In the Hymenoptera floral association study, connectance and weighted network nestedness were low: 0.354 and 0.292 respectively (Table 1). Species-level d' specialization from this Hymenoptera capture indicated that Ichneumonidae, the parasitic wasp family, was the most specialized (Table 2), although this family had the smallest sample size. *Bombus* was the most generalist in its flower preferences, while Apidae at the family level and *Apis mellifera* (honey bees) were relatively generalist as well (Table 2). We also measured the species-level specialization of the plant species that we collected pollinators from in the Hymenoptera floral association study. We found that most species appeared to be generalist in their interactions with pollinators, except for *B. obtusifolia*, *Miconia sp.*, and *O. grandiflora*, which were more specialized (Table 3).
Figure 2: Each species caught during the Hymenoptera floral association study. Images a-e are species caught from the family Apidae; images f-g are members of Crabronidae; h-k are from Halictidae, and l is from Ichneumonidae.

Mark-recapture Study

Fifteen individuals were marked on transect 1, 42 individuals on transect 2, 17 on transect 3, and 12 on transect 4. Of these, 10 (67%) were recaptured on transect 1, 14 (33%) on transect 2, 8 (47%) on transect 3, and 4 (33%) on transect 4. Of all of the foragers that we were able to recapture, they were always found the second time on the same flower species that we caught them on during the marking effort the previous day.

In the mark-recapture study network, both connectance and weighted network nestedness were high, at 0.700 and 0.892 respectively (Table 1). We also measured species-level specialization of the bee pollinators that we marked, as well as specialization of the six plant
species from which we identified and collected the bees. *Apis mellifera* (honey bees) were almost completely generalist, with a substantial sample size (Table 4). We only marked and recaptured two other bee pollinators, and both were from a species in the family Halictidae (Figure 2-i). It also seemed to be quite generalist in its foraging habits according to the d’ output (Table 4), however, we only caught, marked, and recaptured two of these individuals, compared to the 74 honey bees that were marked and recaptured. Finally, all of the flower species that we collected bees from appeared to be generalist, aside from *Miconia sp.*, which we did not recapture any individuals on after they were marked (Table 5). Comparatively, the sample sizes from all species but *A. pseudochilca* were small, as this species was overwhelmingly preferred by honey bees. *Ageratina sp.*, *Dendrophorbium sp.*, and *G. reticulata* had outputs of 0, indicating complete generalization in their interactions with pollinators (Table 5).

**Table 1**: Outputs for connetance and weighted network nestedness for analyses of the mark-recapture and Hymenoptera floral association networks.

<table>
<thead>
<tr>
<th>Network</th>
<th>Connectance</th>
<th>Weighted Network Nestedness</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mark-recapture Study</td>
<td>0.700</td>
<td>0.892</td>
</tr>
<tr>
<td>Hymenoptera Floral Association Study</td>
<td>0.354</td>
<td>0.298</td>
</tr>
</tbody>
</table>
Table 2: Species-level specialization of pollinators from Hymenoptera floral association study

<table>
<thead>
<tr>
<th>Pollinator</th>
<th>d’</th>
<th>Sample Size (number of individuals caught)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apidae</td>
<td>0.341</td>
<td>4</td>
</tr>
<tr>
<td><em>Apis mellifera</em> (honey bee)</td>
<td>0.352</td>
<td>51</td>
</tr>
<tr>
<td><em>Bombus sp.</em></td>
<td>0.071</td>
<td>8</td>
</tr>
<tr>
<td>Crabronidae</td>
<td>0.541</td>
<td>3</td>
</tr>
<tr>
<td>Halictidae</td>
<td>0.511</td>
<td>4</td>
</tr>
<tr>
<td>Ichneumonidae</td>
<td>0.868</td>
<td>2</td>
</tr>
</tbody>
</table>

Table 3: Species-level specialization of plant species from Hymenoptera capture

<table>
<thead>
<tr>
<th>Plant species</th>
<th>d’</th>
<th>Sample Size (number of times visited)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ageratina pseudochilca</em></td>
<td>0.280</td>
<td>43</td>
</tr>
<tr>
<td><em>Baccharis obtusifolia</em></td>
<td>0.717</td>
<td>2</td>
</tr>
<tr>
<td><em>Dendrophorbium sp.</em></td>
<td>0.154</td>
<td>8</td>
</tr>
<tr>
<td><em>Gaultheria reticulata</em></td>
<td>0.189</td>
<td>11</td>
</tr>
<tr>
<td><em>Ilex</em></td>
<td>0.025</td>
<td>4</td>
</tr>
<tr>
<td><em>Monnina pycnophylla</em></td>
<td>0.000</td>
<td>1</td>
</tr>
<tr>
<td><em>Miconia sp.</em></td>
<td>0.771</td>
<td>3</td>
</tr>
<tr>
<td><em>Oreocallis grandiflora</em></td>
<td>0.647</td>
<td>1</td>
</tr>
</tbody>
</table>

Table 4: Species-level specialization of pollinators from mark-recapture study

<table>
<thead>
<tr>
<th>Pollinator</th>
<th>d’</th>
<th>Sample Size</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Apis mellifera</em> (honey bee)</td>
<td>0.025</td>
<td>74</td>
</tr>
<tr>
<td>Green Halictid (Fig. 2-i)</td>
<td>0.110</td>
<td>2</td>
</tr>
</tbody>
</table>
Table 5: Species-level specialization of plant species from mark-recapture study

<table>
<thead>
<tr>
<th>Plant species</th>
<th>d’</th>
<th>Sample Size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ageratina pseudochilca</td>
<td>0.004</td>
<td>59</td>
</tr>
<tr>
<td>Ageratina sp.</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Dendrophorbium sp.</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Gaultheria reticulata</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>Ilex</td>
<td>0.045</td>
<td>7</td>
</tr>
<tr>
<td>Miconia sp.</td>
<td>n/a</td>
<td>0</td>
</tr>
</tbody>
</table>
Bipartite Networks

Figure 3: Bipartite network connecting bee and wasp pollinators from the Hymenoptera floral association study to the flower species that they were found foraging on. Length of the light purple rectangles on the left is proportional to the number of times each flower was seen. Thickness of line that links the plants with their pollinators is proportional to the number of individual pollinators that visited that species of plant. Length of the dark purple rectangles on the right in is proportional to the number of individual pollinators that were marked and recaptured.
**Figure 4**: Bipartite network connecting bee pollinators with the flowers that they were both marked and recaptured on as all of the recaptured pollinators were found on the same species where they were initially found foraging. Only individuals that were recaptured are portrayed here, and the plant they are connected to is the species that they were both marked and recaptured on. Similar to Fig. 3, length of the dark purple rectangles on the right is proportional to the number of individual pollinators from the given family or species that were caught in the overall survey. Length of the light purple rectangles on the left in both figures is proportional to the number of times each flower was seen. ‘Green halictid’ represents two individual morphospecies in Halictidae that we were unable to identify to the species level.
DISCUSSION

Overall, we found that our Hymenoptera floral association network appeared to be much less resilient to ecosystem stressors than our mark-recapture network. When comparing the two, the Hymenoptera floral association network can be interpreted as an extrapolated view of the entire community due to the diversity it incorporates, whereas the mark-recapture was much more narrowly focused on particular individuals. We initially hypothesized that honey bees would be more generalist at the species level in their foraging habits than the native bees and wasps. This was true in our mark-recapture network, but not in the Hymenoptera floral association network. We also thought that native bees and wasps would exhibit higher levels of plant species fidelity than honey bees, but we found all of the pollinators recaptured on the same flowers that they were foraging on when marked, showing high fidelity despite whether or not the pollinator was native. Finally, we hypothesized that both networks would be stable due to high interconnectivity and nestedness between generalists and specialists, but ultimately found that the mark-recapture network demonstrated resilience to disturbance while the Hymenoptera floral association network did not.

Network Resilience

A high connectance in our mark-recapture study network indicated that each plant in the network is connected to multiple pollinators, which increases redundancy and strengthens network robustness to pollinator extinction (Memmott et al., 2004). The high connectance of the mark-recapture network is consistent with our observations, since the overwhelming majority of individuals that we recaptured were honey bees, which exhibited generalist behavior by visiting every single plant species that we surveyed. In contrast, connectance was likely low in our Hymenoptera floral association network because of the increased diversity in this sample, where
four bee and wasp families were represented. This greater diversity of interacting species could lead to greater competition for resources or niche partitioning, increasing specialization and reducing connectance (Valido et al. 2019). In some cases, the presence of honey bees can even replace interactions that could have occurred between the plants and their native pollinators, which also can result in lower connectance overall (Valido et al. 2019). Further, if honey bees were already overcompensating for these lost interactions, then the value of connectance should be high (Valido et al. 2019). Our measure of weighted nestedness in the mark-recapture network was high, but this could be a sample size artifact. The value for weighted nestedness was much lower for the Hymenoptera floral association network. Again, this contrast was expected, because honey bees are known to decrease weighted network nestedness because of their negative effect on low-specificity, rare interactions (Valido et al. 2019).

At the plant level, specialization was very low for those species we found bees on in the mark-recapture study, and, in some cases, such as for Ageratina sp., Dendrophorbium sp, and G. reticulata, a value of 0 for d’ indicated complete generalization. Specialization was also very low for the bees we marked and recaptured, even though the sample size for native bees, which tend to be more specialist in their foraging habits (Waser & Ollerton 2006), was very low. We found low specialization at the species level for both plants and pollinators in the Hymenoptera floral association network, which suggests that the species themselves are relatively generalist in their interactions (Dormann et al. 2019). In some cases, though, specialization appeared to be high, as for Ichneumonidae, B. obtusifolia, and Miconia sp., but these results may have stemmed from the comparatively smaller sample sizes for those groups.
Conclusions

Interestingly, while we found that the honey bees as a species were generalist in terms of the flower species they foraged on (represented by the fact that they were connected to five of the six focal flower species), we also found that every single individual that was recaptured was found on the same species of flower where it was initially marked. In some cases, honey bees were even recaptured in the same flower patch. This suggests that honey bees are specialists at the individual level but not the species level. This result is not especially unusual, as we know that honey bees will recruit nest mates to foraging patches (Balbuena et al. 2012), and they also quickly learn how to forage on particular flower species (Seeley & Visscher 1988), which is why we might still expect high fidelity at the individual level. Floral constancy has been observed among bee pollinators in other studies as well, where pollinating species will restrict their visits to flowers of a single species, sometimes even bypassing more rewarding flowers in the process (Waser 1986). Floral constancy is a behavior that is known to be pervasive in honey bees (Amaya-Márquez 2009) especially, which is especially intriguing given that they are generalists and are able to adapt to seasonal variations and daily floral landscapes if necessary (Amaya-Márquez 2009; Waser 1986).

Other studies have found high plant fidelity among native bees at the individual level, however, as a community there may be increased diversity in their floral preferences (Cecala & Rankin 2020). Our results showed high fidelity at the individual level of native bees, which is demonstrated by the two Green Halictid individuals being recaptured on the same flower species that they were marked on. Halictid bees are broadly recognized as floral generalists, but their fidelity at the individual is largely uninvestigated (Cecala & Rankin 2020), and future studies utilizing the mark-recapture method to measure floral fidelity of native bees should be
conducted. Our recapture rates were quite high compared to the literature (Cecala & Rankin 2020; Peakall & Schiestl 2004; Thorp & Leong 1998; Yamamoto et al. 2014), which indicates that bees and wasps tended to forage in the same areas each day. Pollinators’ repeated return to the same foraging area has been seen in the literature before (Ogilvie & Thomson 2016), especially in patches that are made up of many conspecific plants (Amaya-Máquez 2009), as they were on our transects.

Broader Implications

Our mark-recapture network indicated that the overall plant-pollinator community of the high Andes scrub habitat is relatively resilient to ecosystem stressors, since current theory suggests that mutualistic interactions with low specialization and high connectance and nestedness translate to resilience against species loss due to disturbance (Bastolla et al. 2009; Okuyama & Holland 2008; Valido et al. 2019). However, our results were based on a network that is highly dominated by honey bees, which complicates the findings since honey bees have been found to both replace (Goulson 2003; Valido et al. 2019) and augment (Goulson 2003; Gross 2001) the ecosystem services provided by native bees, and the functional niches they occupy, so this result is not exactly positive. Therefore, our results from the Hymenoptera floral association network, which indicated low connectance, nestedness, and specialization, may be a more accurate depiction of this community’s lack of resilience to ecosystem stressors, as greater diversity was represented in this data through a larger sample size.

Overall, this study is significant because it is essential to know what role insect pollinators play in the larger web of community interactions, including mutualisms, if we are to assess their vulnerability to further disturbance. This information can be used to target future conservation measures based on the network vulnerabilities. Our results contribute insights into
the plant-pollinator interactions in this diminishing and fragmented habitat, and provide a better understanding of the functional role that honey bees occupy in habitats where they are introduced. In the future, it would be interesting to compare our findings to those from similar studies conducted in a tropical lowland habitat, to see if there are any results that are unique to different elevational gradients. Finally, future studies with larger sample sizes incorporating more native pollinators would be beneficial to validate our findings and to uncover more of the nuanced relationships between plants and their pollinators, particularly within habitats that are vulnerable to various stressors.
Literature Cited


Dormann CF, Gruber B, Fründ J (2019) Introducing the bipartite package: analysing ecological networks. interaction 1:0.2413793


## SUPPLEMENTARY DATA

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