Pollinator community structure and interactions on *Monardella odoratissima* spp. *glauca*

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**ABSTRACT**

Pollinator floral resources may be limiting, as they are often patchy and used by many pollinator species. In subalpine communities, these limitations may be exacerbated by the short growing season and constrained phenology of many plants. *Monardella odoratissima* spp. *glauca* is one of the few flowering plants with plentiful resources for insect visitors which remain in bloom during the dry summer of the White Mountains in south-eastern California. The lack of competitors allows this generalist to provide resources to the majority of the diverse local pollinator community. We expect the limited availability of flowers to induce aggressive behavior between visitors of *Monardella*. We predicted *Monardella'*s diverse visitors would cause the pollinator network to become nested into predictable subgroups based on species diversity, an ecological concept of community ecology with implications for community-wide stability and resilience. Through observing the pollinator networks and behavior upon *M. odoratissima*, results showed a highly nested structure and differentiation in behavior based on species or genus. Our findings offer better understanding of the complex structure of pollinator networks and the interactions that occur within them.

Keywords: mutualism, nestedness, pollination network, community ecology, competition

**INTRODUCTION**

One of the main tenets of ecology is to understand the complex systems of interspecies interactions at the community and population levels. Three-fourths of the world’s flowering plants and almost half of all agricultural crops depend on plant-pollinator interactions for survival and reproduction (NRCS n.d.). Most flowering plants are able to self-fertilize yet still rely on pollinators to increase gene flow and minimize the consequences inbreeding (Jabis 2011). Understanding the communities of pollinators and visitors, in relation to the flowering plants they visit, has important implications for both parties in these mutualistic interactions. The reproductive success of popular generalist plants, in particular, is fueled by the interactions and behaviors composing a wide network of pollinators. Many variables contribute to visitor behaviors and interactions such as time of day, local
weather patterns, flower density and morphology, number of flowers or inflorescences available for pollination, and resource availability (Field 2005). This study aims to develop an understanding of these pollinator networks as well as the environmental and behavioral factors that drive these interactions.

Many pollinator networks display varying degrees of nestedness, meaning the species composition within the community consists of a non-random structure in which a subset of visitors in species-poor areas are nested inside a larger group of species present in species-rich sites (Ulrich 2012). This definition suggests a predictable spectrum of species richness across sites. Nestedness is commonly examined within mutualistic interactions between flowering plants and their pollinators and has important implications for community survival and resiliency (Ulrich 2009). Ulrich also reports that a highly nested structure describes species distribution in relation to resources, while a non-nested network is randomly assigned (2009). Generalist plant species that attract a wide array of visitors may be particularly likely to exist within nested pollinator subgroups.

In this study, we surveyed pollinator presence and behavior of the widespread Monardella odoratissima spp. glauca (hereafter referred to as Monardella), an extreme generalist and one of the few blooming plants available to pollinators during the dry season. This caused an influx of diverse visitors to this generalist flower. This study aims to classify behavioral interactions and structure of the pollinator networks present on the abundant Monardella, specifically those found in mutualistic interactions. We hypothesize that behavior will depend on species, time of day, and number of available inflorescence per patch. Additionally, we expect to find the pollinator network upon Monardella to be nested in terms of species diversity as it attracts a diverse group of visitors.

METHODS

2.1 Study System

Research was conducted at White Mountain Research Station north of Bishop, California from August 2–August 5, 2018. The White Mountains are a subalpine ecosystem dominated by limber (Pinus flexilis) and bristlecone (P. longaeva) pine, with a shrub layer dominated by several species of sagebrush (Artemisia tridentata ssp. californica) and rabbitbrush (Chrysothamnus viscidiflorus). We examined Monardella on the granitic slopes of the Crooked Creek Research Station at various elevations of approximately 3000 meters. An array of pollinators and visitors appeared to rely heavily on the flowering plant, as it is one of the few flowering plants available during the dry summer season. Several days of rain and hail previous to this study resulted in lessening average flower density per patch, possibly making pollen a limited resource in the local community. Monardella inflorescences consists of a multi-flowered head of small upward facing flowers. The petals of the flower are purple and fused at the base forming a tubular corolla. Although the flowers themselves are not particularly aromatic, as a member of the Lamiaceae family, its foliage is very aromatic and produces a pungent minty smell.
2.2 Field Methods

We conducted an observational study focusing on the interactions between visitors on 60 patches of Monardella. Patch size was quantified as the number of inflorescences with live flowers available for pollination. Size ranged from two to seventy-one inflorescences per patch. Density was measured by quantifying number of flowers per inflorescence as low, medium or high. These categories were based on percentage of flowers remaining on the inflorescence; low denoting about 30% of flowers remaining, medium 30–60%, and high with almost all flowers remaining. Flowers were lost primarily due to rain and hail previous to surveys. All patches were observed in increments of 30 minutes, occasionally surveyed twice, totaling one hour. Patches were observed from 9 am to 5 pm each day, with few pollinators found before or after these hours. Unknown visitors were caught and identified in the lab. We classified three distinct interactions which could take place between visiting insects: aggression, avoidance and tolerance. Aggression denotes a visitor which flies directly towards another or chases them off an inflorescence. Avoidance was defined as a visitor fleeing in the presence of another or flying towards a choice inflorescence, but diverting due to presence of another. Tolerance was multiple visitors coexisting upon the patch without interacting directly.

2.3 Statistical Methods

We used JMP version 14 for all statistical analyzes unless otherwise noted. We used a multiple regression to test time of day on visitation rate. In order to test if visitation rates were the highest in the middle of the day we used a quadratic regression. We modeled total visits across the more common species: Hyles lineata, Bombus huntii, and Bombus flavifrons, along with Hymenopteran genera, Anthophora, Osmia and Bembix, and the fly order, Diptera. We used an ANOVA test to the effect of flower density on species richness. We used the NeD ecosoft nestedness matrix to test the nestedness within this specific community as compared to a null matrix of the same size.

RESULTS

There was a correlation between time of day and visitation rates following a parabolic pattern. Visitation rates increase from 9:00 am until peaking around 12:30 pm, then slowly decline for the rest of the day (R=0.21, N=64, Ppatch size <0.01, Ptime =0.02; Figure 1). We found that the times of heaviest visitation over the course of the day were variable between different species. Each taxon demonstrated different patterns of visitation but many followed a bimodal pattern with a heavy visitation peak earlier on in the day, between 10:00 am and 11:00 am, and a second peak later in the day (R = 0.02, N = 340, P < 0.002; Figure 2). Behavior was highly variable among taxa. Anthophora, a species of bee, exhibited more aggression and less tolerance than any other taxon. Avoidance was most common in Osmia and other species of Diptera; while tolerance was relatively high in wasps, Bombus species, and Lepidoptera (Figure 3). Despite being the largest visitor requiring more resources, hawkmoths showed little behavior other than tolerance.
Figure 1: Visitation rate by time of day. The x-axis represents time of day in military time. Visitation rate is the number of visits per flower, per hour. Visitation increased at the start of the day, peaked around 12:30, followed by a gradual decrease until the evening (n = 85).

Figure 2: Taxon specific visitation by time of day. The x-axis represents time of day in military time, y-axis showing desired taxon. Thickness of contours represents total number of visits (n = 340).

Figure 3: Taxon-specific behavior. Different taxon display different behavior when visiting a plant. Three behavioral classifications are aggression, avoidance, and tolerance; behavior was recorded whenever two or more visitors interacted. The basis for each interaction is defined in Methods (n = 91).

NeD nestedness software reported this community was highly nested compared to a null matrix, in which the insects visiting low density patches consisted of a predictable subset of the more dense patches. (N = 455, F = 39.5, P < 0.001; NODF 65.069, P > 0.0001; Figures 4 & 5).

Figure 4: Species richness by flower density. Plots with low flower density had lower species richness, showing that low density plots consist of predictable subsets of visitors present at medium and high density plots.
DISCUSSION

4.1 Resource Sharing

We found over 50 taxa that visit Monardella throughout the day, some overlapping in visitation times and others showed opposite patterns of visitation than competing species (Figure 3). The insect visitors of generalist flowers, like Monardella, compete with other species for floral resources. Resource competition can be mitigated by partitioning of temporal niches for foraging throughout the day. Insects must also adhere to their own physiological limitations against environmental factors like temperature, humidity, precipitation and wind, restricting the times of the day that they can forage (Barônio and Torezan-Silingardi 2016). Past studies have looked at the trade-off between having a unique temporal niche and access to a greater supply of resources and accounting for suitable environmental conditions. Barônio and Torezan-Silingardi’s study found the abundant presence of temporal niche overlap of similar insect species, which showed that foraging during hours of optimal abiotic conditions may be more important to flower visitors than the foraging during times of least competition and most abundant resources. We found similar niche overlaps in our taxon visitor timelines. The similarity of the visitation contours of taxa like Bembix, Anthophora and Diptera may indicate a similar resistance or susceptibility to certain conditions. On the other hand, we found some taxon with oppositely shaped contours, like those between Hyles lineata and Osmia, which may indicate varied requirements for resources and the temporal limitations of those resources in Monardella (Figure 1). Earlier studies have also attributed bimodal visitation patterns of pollinators to the extreme heat and humidity at the middle of the day (Barônio and Torezan-Silingardi 2016). Although our overall flower visitation rates show the highest visitations at around 12:30 pm (Figure 3), several of our visitors, Anthophora, Bembix, Bombus huntii, and Diptera, show a similar bimodal pattern, dipping at around 12:30 pm (Figure 1). Overall, our temporal visitation contours through the course of the day shows varying patterns between taxon which may explain how so many different species are able to share this same resource in the Monardella.
4.2 Visitor Interactions

Most of the interactions observed among pollinators on *Monardella* were tolerant. Of the species that demonstrated aggression, Anthophora was the most aggressive towards other visitors while wasps, *Bombus* species, and Lepidoptera exhibited the greatest amount of tolerance. Many of the *Bombus* species appeared to be aggressive only when provoked by another visitor or when competing for a specific flower. We observed a species of *Bombus* pollinate the same patch as another common visitor multiple times, a behavior which appeared to be common among the genus.

The most common behavioral interaction was tolerance. Some species may be naturally more aggressive, while others may be more aggressive under certain circumstances (Amselem and Hefetz 2010). Aggression varies by time of year due to differences in climate or weather conditions (Cane and Payne 1993). Aggression was a relatively rare interaction, despite competition for a seemingly limited resource.

4.3 Nestedness

The pollinator network present upon *Monardella* flowers was highly nested compared to a null model (Figure 5), indicating that community structure was neither randomly organized nor compartmentalized but consisted of varying groups nested within one another (Bascompte 2003). Patches with low flower density had lower species richness than those with higher density, illuminating the predictable subset of visitors present at medium or high density plots (Figure 4). The underlying cause of these nested subsets of visitors remains controversial throughout literature, but may be constructed by relative species abundance (Krishna 2008) or species richness (Bascompte 2003). Strong nestedness has been found to have many positive benefits for both the structure and individual members of a community, such as robustness, or resilience, to disturbance or lost species, ability to host rare species, and tolerance to extinction (Bascompte 2003, Vanbergen 2017). Understanding the complex structures of a nested pollinator network aids in our understanding of the roles of plants and pollinators in the community, and how these non-random patterns can reduce species’ risk of extinction. If pollinator behavior or populations fluctuate, the plants which depend on them suffer from inbreeding and other reproductive loss due to lacking gene flow and pollen shortage (Field 2005). Studies have shown high levels of nestedness allow a community to better adapt to disturbances such as local extinctions and increase overall stability (Vanbergen 2017). Plant-pollinator mutualism promotes effective plant reproduction, which benefits both the plant and whomever pollinates it.

4.4 Future Studies

Future studies could examine the pollinator networks of *Monardella’s* neighboring plant species, comparing overlap and differences between local species. Expanding on this topic would give us a better understanding of pollinator behavior and niche partitioning within different pollinator networks, particularly in areas of high climate intensity. Repeating
this study during another season may show temporal variation in behavior, illuminating new interactions and behavior based on resource abundance or scarcity. Conducting this study during the wet season may decrease the window for optimal pollination, thus causing more interactions.

Further quantifying and understanding these complex structured communities and the behavior within them helps us to better understand the many interactions that go on within a given pollinator network. We hope our study can be used to further knowledge of pollinator behavior and the species composition within a community.

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REFERENCES


