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EFFECTS OF MECHANICAL HABITAT DISTURBANCE ON THE DIVERSITY AND
NETWORK STRUCTURE OF PLANT-BEE INTERACTION NETWORKS IN CENTRAL
FLORIDA

by

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B.S. University of Central Florida, 2011

A thesis submitted in partial fulfillment of the requirements
for the degree of Master's in Science
in the Department of Biology
in the College of Science
at the University of Central Florida
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ABSTRACT

Ecological interactions within a community shape the structure of ecosystems and influence ecosystem function. Plant-pollinator interactions exist as mutualistic exchange networks that may collapse as habitat loss occurs, thereby threatening the overall health of an ecosystem. Understanding the impacts of human-mediated habitat disturbance on ecological interactions is therefore crucial for conservation efforts. Archbold Biological Station (ABS) in Venus, Florida contains over 2000 hectares of protected Florida scrub habitat nested within a human-dominated environment that is threatened by anthropogenic habitat disturbance. In past studies, over 113 bee species and 157 associated host plants, many endemic to the Lake Wales Ridge, have been found on ABS property, providing an understanding of this system's plant-bee network. Using those data as a baseline, this study investigated the effects of varying levels of mechanical habitat disturbance intensity on the diversity and network structure of plant-bee interaction networks. Flowering plant abundance, richness, diversity, and composition as well as bee abundance and composition were significantly different across mechanical habitat disturbance levels. Interactions between bees and flowering plants also differed with varying disturbance intensity. From these results, it is clear that plants, bees and interactions between them are impacted by mechanical habitat disturbance in this system. This project informs management efforts not only for natural systems with the threat of alteration, but also for agricultural systems, many of which heavily rely on flower visitation by bee pollinators. This research also contributes to the growing field of interaction ecology by increasing understanding of habitat alteration effects on a valuable ecological interaction and ultimately ecosystem function.

I dedicate this work to the wonderful planet, which has hosted my research and my being.

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LIST OF ABBREVIATIONS

ABS	Archbold Biological Station
ANOVA	Analysis of Variance
FFWCC	Florida Fish and Wildlife Conservation Commission
GIS	Geographic Information Systems
LWRWEA	Lake Wales Ridge Wildlife and Environmental Area
NMDS	Non-metric multidimensional scaling

CHAPTER 1: INTRODUCTION

An ecological interaction is the relationship of an organism to others in a community and is therefore important for biotic ecosystem function. Interactions may be mutualistic (beneficial to both), commensal (beneficial to one while the other is unaffected), competitive (both species are negatively affected), or predatory (one species benefits while the other is harmed). The accumulation of species interactions results in an interaction network, an example of which is a plant-pollinator web. Interaction networks in a community contribute to overall ecosystem function by shaping the structure of species-interactions within a community. In the case of a plant-pollinator interaction network, plant visitors interact with certain flowering plants, and floral rewards are often exchanged for pollination services. The majority of flowering plants rely on these pollination services by flower-visitors such as insects for reproduction and gene flow (Hamrick 1982). Pollination generally occurs when wind, water, insects, birds, or mammals transfer pollen from one plant to another. In the case of animal-mediated pollination, a pollination event occurs when pollen taken from the anthers of a flower are deposited to the stigma of another flower by the pollinator. During this process, a nectar reward is usually provided by the flower to encourage visitation to its reproductive parts (Heithaus and Raymond 1974). Without such interactions, those plants that rely on animal-mediated pollination cannot receive the pollination service they need to produce seeds. If a flowering plant relies on a specific interaction with one pollinator and that pollinator is lost, the likelihood of the survival of that plant species is low.

Plant-visitor interactions are considered mutualistic because the interaction usually benefits both the plant and the visitor. Interactions between plants and animals in an ecosystem have driven much of the biodiversity we see on the planet today (Bascompte and Jordano 2007).

These combined interactions can be quantified and used to describe how individuals in a system are linked. Most interaction networks have many species, with overlapping interactions, and are complex in structure as a result (Bascompte and Jordano 2007). The complexity of these networks contributes to ecosystem diversity, stability, resistance, resilience, and functionality (Bascompte and Jordano 2007).

Habitat change driven by anthropogenic disturbance is a threat to the existing biodiversity on Earth because it disturbs or eliminates the available environment in which organisms live. Increased frequency of human-mediated habitat disturbance has resulted in alteration and/or loss of suitable habitat for plants and their associated visitors. The impact of habitat fragmentation on plant-visitor networks is currently uncertain (Deyrup et al. 2002, van der Putten et al. 2004, Tylianakis et al. 2007). Fragmented areas are expected to host fewer pollinators due to a lack of ideal resources available for flower visitors, which ultimately impacts those flowers that rely on pollinator visitation for reproduction (Lennartsson 2002). Anthropogenic habitat disturbance is therefore expected to have an impact on flower visitation choices of potential pollinators. Human-mediated habitat alteration and subsequent biodiversity reduction has the potential to severely impact plant-pollinator interactions and the service of pollination through disruption of network structure (Fontaine et al. 2006). If a plant or pollinator becomes extinct locally due to human-mediated habitat disturbance, or is separated by habitat fragmentation, natural pollination services may be lost for those individuals.

Anthropogenic habitat disturbance is changing suitable habitat for plants and pollinators faster than adaptation can compensate for in these networks (Aizen and Vazquez 1998). As a result, the composition, function, and overall performance of plants and visitors are expected to differ across natural and altered systems (Aizen and Vazquez 1998). If a system is very diverse,

it is more likely to have a variety of ecological interactions between species that exist in that system. With increased human-mediated habitat disturbance, species may be lost from an area and as a result, the interactions that species share will be lost from the network. For example, if an area has a flower diversity of 30, there may be a wide array of flower-visitor interactions with multiple pollinator species that exist in the vicinity but if that area is disturbed and is reduced to a flower diversity of 5, it may be less desirable to flower-visitors.

It is therefore important to understand how continued human-mediated habitat change will impact the presence of potential interacting players in a network. Such consideration will contribute to efforts to conserve the valuable ecosystem service of pollination. If the structure of interactions between plants and pollinators change, this could negatively affect an entire ecosystem. Alteration may impact presence of plant and visitor species in a system as well as characteristics of plants and visitors, such as phenology (flowering life cycle) or resource availability respectively. This will ultimately influence pollination services and the fitness of those individuals within the network which may degrade ecosystem function (Vazquez and Aizen 2003).

In summary, ecosystem function and stability depend greatly on the presence and reliability of interactions between individuals in a community. Understanding how the dynamics of network structure influence these interactions is limited (Blüthgen et al. 2007). This study will examine all flowering plants and their associated bee visitors in reference and disturbed sites for a year to investigate whether diversity and network structure of plant-bee interaction webs differ with varying levels of mechanical disturbance intensity. Bees were chosen because they are indicator species that are sensitive to changes in the environment. Plant-bee interaction networks are also understood to be very diverse with a multitude of interacting plants and bees (Deyrup et

al. 2002). Plant-bee networks were also chosen as the interaction network for this study because observing plant-bee interactions was minimally-invasive to the current state of the study area. Study sites needed no further disruption than presence of the researcher for sampling. Network stability determines the response of a community to change. As landscapes continue to undergo alteration, the stability of these communities will be tested (Fortuna and Bascompte 2006).

Methods

This study was conducted at Archbold Biological Station (ABS), a long-term ecological research facility located in Venus, Florida that was established in 1941 (Figure 1). The station has become an internationally recognized research station that includes a portion of protected habitat at the southern tip of the Lake Wales Ridge, which is an elevated sand dune ridge with a maximum elevation of 95 meters created during the Pleistocene epoch. The isolation of the area during higher sea level resulted in rare habitat formation with many endemic species. The ridge runs north to south through Central Florida for about 240 kilometers. ABS consists of 2,101 hectares of actively managed, natural Florida scrub habitat, xeromorphic scrub, and pine flatwoods (Menges et al. 2007). The station is dedicated to performing research that informs efforts to understand and preserve this delicate ecosystem, much of which is threatened by habitat change. As much as 80% of the Lake Wales Ridge has been altered by fire suppression, clear-cutting, mechanical disturbance and non-native species invasions (Turner et al. 2006). The effect of these disturbances on habitat composition, structure, and functioning is not fully understood.

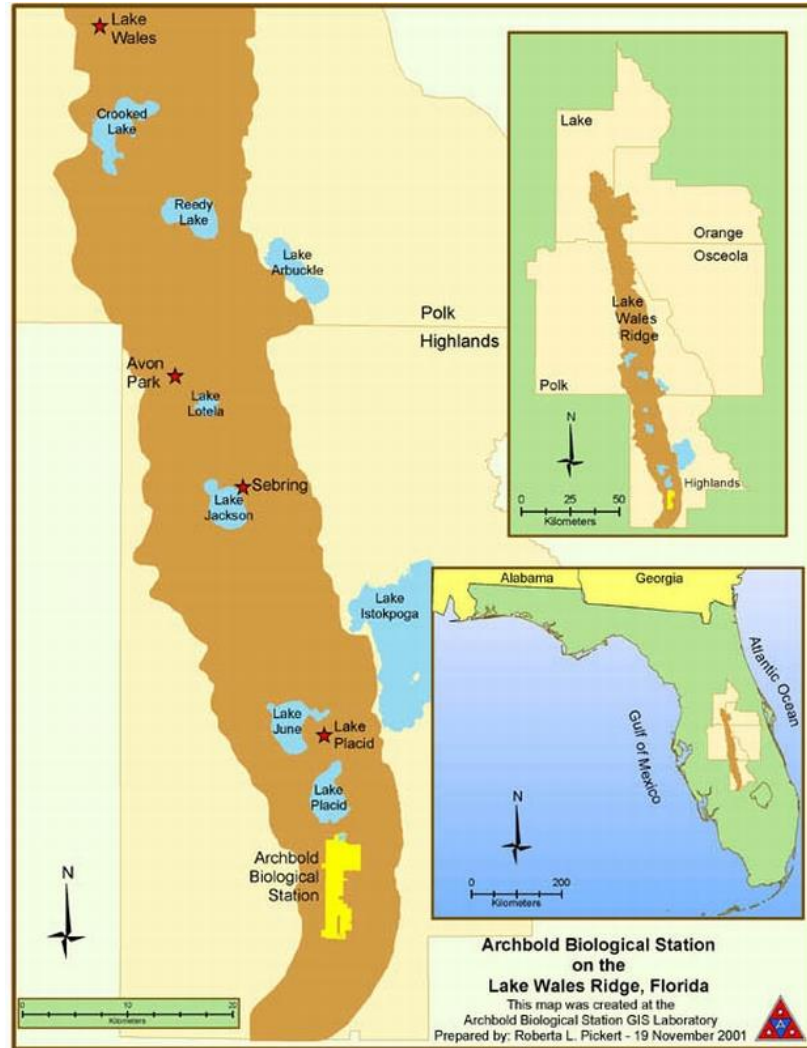


Figure 1. Map of Florida showing location of the Archbold Biological Station, Venus FL in yellow.

Adjacent to ABS, the Archbold Reserve is a 1,476 ha conservation area. The reserve consists of completely altered lands that have been converted to pasture from scrub habitat. Another area used in this study, the McJunkin Tract, was acquired in 2002 by the Florida Fish and Wildlife Conservation Commission (FFWCC) and is part of the Lake Wales ridge Wildlife and Environmental Area (LWRWEA) that is adjacent to the northwest portion of the main ABS property. The area was previously used for cattle grazing. Portions of both the Reserve and the McJunkin Tract are currently undergoing experimental restoration to remove non-native plants,

restore scrub-plant densities, and reestablish native species composition and ecosystem function (Menges et al. 2007).

Deyrup et al. (2002) developed and maintained a long-term survey of bees at ABS to determine the network of bee species and the flowering plant species they visit on the station. They recorded 113 bee species and 157 associated plant species. Only one bee species (the European honey bee, *Apis mellifera*) is non-native (Deyrup et al. 2002). Based on the long-term surveys conducted by Deyrup et al. (2002), there is an understanding of the interaction network of plants and bees at ABS. Using those data, an interaction matrix containing 113 bee species and 157 plant species was analyzed using the *bipartite* package for R (Dormann et al. 2008, 3.0.3, R development core team 2013) to construct a network graph (Figure 2). This graph displays the complexity of the known plant-bee interaction network at ABS, as it is based on 20+ years of data, but has no resolution spatially or temporally because methods for gathering data on plant-bee visitation events were haphazard as the study aimed to develop an understanding of the overall plant-bee visitation network.

These data were valuable for developing an understanding of the general plant-bee network in this system and for developing research questions for this project. Deyrup et al. (2002) discussed the possibility that habitat alteration may be a factor in the presence or absence of bees, which should have an effect on the overall network. Using those data as a baseline, I explored the diversity of plants and bees as well as plant-bee interaction network structure in Florida scrub habitats that have received varying levels of mechanical disturbance intensity in an attempt to investigate the effects of human mechanical habitat disturbance on plant-bee interactions. Bees were chosen as the plant-visitor taxa for this survey because they are sensitive

to changes in the environment and they are a diverse group that is simple to observe, capture, and identify (Kevan 1999, Deyrup et al. 2002, Droege 2010).

The disturbed sites chosen for this study represent increasing levels of roller chopping intensity. Roller chopping is a form of mechanical disturbance used to clear areas with dense brush. A machine is used to topple small trees and chop shrubs and bushes to reduce their density. This technique is usually employed in an attempt to convert dense scrub habitat into pasture lands for cattle grazing.



Figure 2. Bipartite graph showing plant-bee interactions at Archbold Biological Station. Bee species are represented as the top trophic level, plant species (by number) are on the bottom. Width of the species bars is proportional to the sum of interactions.

This study focused on two major questions. The first question explored is whether the assemblage of plants and bees within a system changed with increased mechanical disturbance intensity (Chapter 2). To answer this question, plots were surveyed for species richness and abundance of plants and bees. Those data were then used to calculate Jost diversity (the number of effective species in a system) and to compare richness, abundance, and Jost diversity across the disturbance levels to determine if there was a significant difference in plant and bee diversity measures with increased mechanical habitat disturbance. Species composition was also investigated to determine whether the assemblage of flowering plant and bee species changed with increased habitat disturbance. It was predicted that all plant and bee assemblages would differ across the disturbance levels.

The second question this research addressed is whether the interactions between plants and bees changed with increased mechanical habitat disturbance (Chapter 3). To do this, the structure of plant-bee interaction networks in each of the disturbance categories was investigated and compared to determine whether mechanical disturbance intensity had an effect on the plant-bee networks in this system. It was predicted that network structure as well as interactions between plants and bees would change with increased mechanical habitat disturbance.

Sixteen total plots were used for this study with four replicates per site type – pasture lands (chopped and mowed), heavily disturbed scrub (chopped multiple times), moderately disturbed scrub (chopped once), and undisturbed scrub (reference sites) (Appendix A). Four plots were located in the southeast portion of the Archbold Reserve, four in the McJunkin Scrub of the Lake Wales Ridge Wildlife and Environmental Area (LWRWEA), four in the pastures of the Archbold Reserve, and four high-quality scrub reference sites in the western section of ABS. Sites chosen for this study were based on previously established plots by Menges et al. (2007)

and used to evaluate the questions posed in this research (Figure 3). Sites have similar elevation, soil type, area, and disturbance histories. All circular plots have a 50 m radius (Figure 4). Each experimental plot was surveyed once a month for a year using two 50 m x 2 m belt transects randomly assigned each survey.

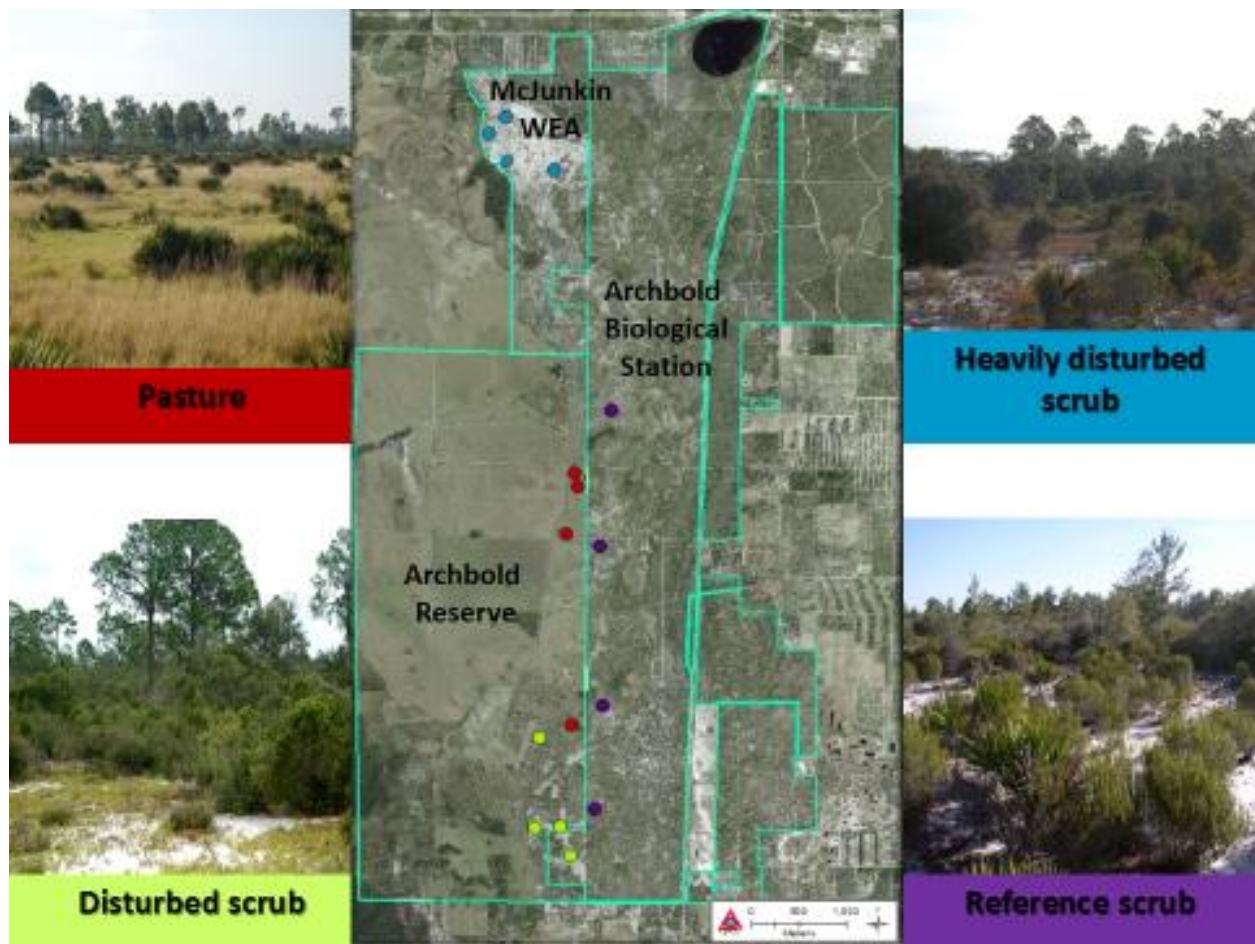


Figure 3. Geographic information system (GIS) Image of Archbold Biological Station showing location of study plots and representative pictures of disturbance types (Menges et al. 2007). Colored dots represent disturbance type.

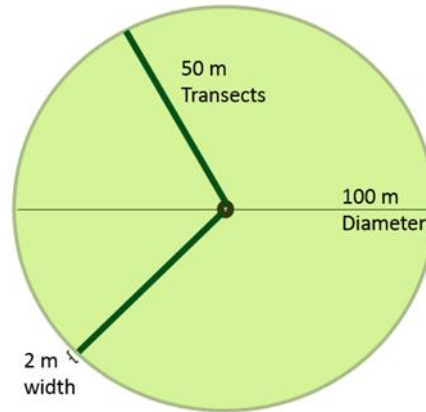


Figure 4. Individual plot design. Transects were assigned random compass bearings from the center to the outer perimeter of the plot.

The pasture plots located on the Archbold Reserve were previously roller-chopped, mowed, and grass-seeded. These areas were historically used for cattle grazing. They are currently dominated by *Paspalum notatum* (bahia grass). The heavily disturbed scrub plots located on the McJunkin tract have been roller-chopped multiple times in the past. The moderately disturbed plots in the southeast scrub of the Reserve have been roller-chopped once in the past. Both the heavily and moderately disturbed sites have patches of non-native *Rhynchelytrum repens* (natal grass) and overgrown scrub oaks (five species in the genus *Quercus*) (Menges et al. 2007). All of the disturbed sites have altered soil composition and structure as a result of grazing and mechanical clearing which is expected to influence the numbers and types of flowering plants that recolonized these areas (Menges et al. 2007). Reference sites are located in undisturbed, high-quality scrub on ABS property. The property is periodically burned in sections based on recommended fire return intervals ranging from 6 to 30 years (Menges et al. 2007).

Data were gathered on the diversity of and interactions between plants and bees at the sites to determine how anthropogenic mechanical habitat disturbance impacted the composition

and structure of plant-bee networks. Plants were identified in the field using *The Guide to Florida Wildflowers* (Taylor 1992). Bees were identified to species using identification keys from *Bees of the eastern United States* (Mitchell 1960 and Mitchell 1962). Plots used for this study did not receive any form of manipulation beyond the presence of the researcher during surveys.

Analyses

Mixed effects modeling in R (3.0.3, R development core team 2013) using the *glmmADMB* package was employed to determine whether modeled response variables [abundance, richness, and Jost diversity (the number of effective species)] of flowering plants and bees across the disturbance levels were similar (Fournier et al. 2014). Mixed modeling was chosen to analyze differences in the response variables because the design of this study included repeated measurements of the same plots each month and it is not sensitive to missing values, of which there were many in this study. The fixed effect was disturbance category (trt). Random effects included month (m) and distance to nearest plot (nds). Akaike information criterion (AIC) was used to rank and identify the best model (Gaussian, Poisson, or Negative Binomial).

$$\mathbf{Response} = \mathbf{trt}_i + \mathbf{m}_i + \mathbf{nds}_i + \boldsymbol{\varepsilon}_j \quad (1)$$

Non-metric multidimensional scaling (NMDS) in PCORD 5 was used to visualize the similarity of bee and plant communities in each of the disturbance categories. It was also used to investigate whether interactions across the mechanical disturbance levels were similar. A NMDS analysis places points farther away from each other the more dissimilar they are (Gotelli and

Ellison 2004). Those points that are more similar to each other are plotted closer together. PCORD 5 was also used to build a distance matrix to numerically determine plant and bee community dissimilarity as well as interaction network dissimilarity. This analysis assigns dissimilarity values between 0-1 where zeroes represent communities that are identical and numbers greater than zero ($>0-1$) represent communities that are increasingly dissimilar the closer the number is to 1.

Observed plant-bee interaction data were recorded in a matrix with bee species as the upper trophic level, and plants as the lower trophic level. If an interaction occurred, the connecting cell between the bee species caught and the plant species visited received a value representing the number of times those species were caught interacting with each other. An example matrix can be seen in Table 5. In this study, if a bee was caught visiting a flower, it received a 1 (or more depending on the number of times that bee species was caught visiting that flower species) in the matrix representing an interaction between trophic levels. If there was no interaction between a plant and bee species, the connecting cell received a zero. It is important to note that certain bee and flowering species may not have been captured during this study as a result of missed interactions, phenology of flowers, habitat type, and/or time of day.

Table 1. Example interaction matrix with zeroes representing no interaction between species and ones representing an interaction.

	Bee A	Bee B	Bee C	Bee D
Plant A	1	1	1	1
Plant B	1	1	1	0
Plant C	1	1	0	0
Plant D	1	1	0	0
Plant E	1	0	0	0

Interaction matrices were analyzed using the *bipartite* package for R (Dormann et al. 2008, 3.0.3, R development core team 2013), to construct network graphs for each disturbance level. If an observed interaction is recorded, the bipartite network displays members of one trophic level, in this case, plants, connected to members from another trophic level, in this case, bees. *Networklevel* is an analysis tool within the bipartite package that performs a variety of network analyses and provides network indices that can be compared such as network specialization or nestedness to understand structural differences between networks as well as measures such as interaction strength asymmetry and robustness to extinction to determine the importance or contribution of species to a network (Dormann et al. 2009). Therefore, performing network analyses using the bipartite package is an effective way to answer the questions posed for this research.

Network specialization is a measure that represents the overall amount of specialization found in the network from both trophic levels. Specialization refers to the diversity of interactions a species is observed to make with species from the opposite trophic level (Devictor

et al. 2010). Those species that interact with only one species from the opposite trophic level are considered highly specialized, whereas those that interact with many are considered generalists. The degree of nestedness represents the amount of specialist interactions that are nested within the interactions of generalists. A network has a high degree of nestedness if those species that interact with only a few individuals (specialists) are subsets of those that interact with many individuals (generalists). Interaction strength asymmetry (dependence) indicates the amount of dependence bees and plants have on each other. For example, due to the heterogeneous nature of plant-bee interactions, if a plant depends strongly on the interaction with a bee visitor, the bee visitor likely depends weakly on the interaction with the plant. Therefore the plant would have a high interaction strength asymmetry since it is highly dependent on the bee for visitation and the bee would have a low interaction strength since it depends weakly on the plant. The last network index used to compare the plant-bee networks in this study was robustness to extinction. This index randomly removes species from a network and measures how robust species left within the network are to extinction without the interactions from the removed species.

It should be noted that while these network analyses are useful for this study and the specific questions asked, there are limitations to the indices used here (Dormann et al. 2009). The indices used may not give results that truly depict true relationships between current plants and bees in each of the networks across disturbance levels because some of the indices used in this study from the *bipartite* package are sensitive to network size, rare species, and sampling intensity (Dormann et al. 2009). However, despite these limitations, these network analyses allow visualization of observed interactions as well as provide insight to changes in specificity of players in the networks which are informative to the questions posed in this research.

In light of this understanding, ordination was used to further investigate the similarity of interaction matrices in this study. Non-metric multidimensional scaling (NMDS) was employed to summarize and compare interaction data in an ordination graph that reveals similar versus dissimilar samples based on their proximity to each other in the graph (Gotelli and Ellison 2004).

CHAPTER 2: DIVERSITY OF PLANTS AND BEES IN HABITATS WITH VARYING LEVELS OF MECHANICAL HABITAT DISTURBANCE

Introduction

Interactions between plants and animals in an ecosystem are imperative for ecosystem function and biodiversity (Bascompte and Jordano 2007). Most interaction networks contain a multitude of species, many of which overlap in their interactions, and are complex in structure as a result (Bascompte and Jordano 2007). This complexity results in increased ecosystem diversity, stability, resistance, resilience, and functionality (Bascompte and Jordano 2007). As the amount of diversity in a system increases, the more functionally constant and therefore resistant to disturbance an ecosystem will be (Winfrey et al. 2007). It is therefore important to explore the diversity of most if not all potential players in a network. It is also important to understand the factors that influence the presence or absence of potential contributors to a network by determining the richness, diversity, abundance and composition of those organisms in a system. Kearns et al. (1998) propose that recent declines in pollinators may be mitigated by performing relevant broad-scale studies to better understand the ecological constraints of plants and their associated pollinators.

Alterations to suitable habitat for plants and pollinators change the environment in which potential players in a network operate. Threats to plant-visitor networks include unnatural habitat destruction and alteration, pesticide and herbicide use, exotic species invasion, and fire suppression (Kearns et al. 1998, Deyrup et al. 2002). As a result, the composition, function, and overall performance of plants and visitors are expected to differ across natural and altered systems (Aizen and Vazquez 1998). Human-mediated habitat alteration may impact plants and/or

visitors in many ways. For example, phenology of a plant (the flowering period) may shift as habitat alteration occurs changing the time of year that a flower comes into bloom. If this occurs, the time that resources are available to plant visitors may also shift, especially if a visitor has a short life span. This may in turn impact the ability of a plant to receive pollination services, particularly if the plant is a specialist and relies on only one or a few visitors for pollination. Another example that directly affects bees is resource availability. If floral resources are scarce as a result of habitat disturbance, bees may have to travel farther distances in order to successfully forage, increasing the costs of gathering those resources (energy use, predation risk, and homing ability). These factors may influence plant-visitation and subsequent pollination services as well as the fitness of those individuals within the plant-bee network. Without the stable operation of ecological interactions such as plant-pollination, ecosystem function may be reduced (Vazquez and Aizen 2003).

Additional factors that may influence presence of flower-visitors in an area include rewards provided by the flower to the visitor, distance and cost of travel to flowers, morphological constraints posed by flowers, and visitor lifespan in relation to flowering period of the plant (Waser et al. 2012). Though multiple species may be redundantly providing the same service that could be provided by one, redundancy serves as an underlying mechanism for ecosystem stability because each species may be capable of responding differently as the environment changes (Winfree et al. 2007). For example, if a plant species has multiple pollinators, the extinction of one of those pollinators due to some environmental change will likely have little effect on the survival and reproduction of the plant since there are multiple visitors. Additional factors that may influence network structure in a plant-visitor web are

phenotype, demography, distribution, dispersal ability, and species composition within a community (Vazquez et al. 2009).

Understanding how human-mediated habitat change influences the diversity of species (potential contributors to interaction networks) is important to guide appropriate changes in land-use practices. If presence of flowering plants and flower-visitors changes with mechanical disturbance, this could negatively affect an entire ecosystem. This study will examine the species richness, abundance, diversity, and composition of flowering plants and bees for all four seasons across mechanical habitat disturbance levels. The results of this study will inform the research in Chapter 3 investigating changes in interactions between plants and bees across mechanical disturbance levels in this system.

Methods

Data were gathered on the diversity of plants and bees at each of the 16 sites to determine how mechanical disturbance intensity impacts the diversity and structure of plant-bee networks. Plant diversity in each habitat type was determined by recording all flowering plants rooted within two randomly assigned 50 m x 2 m transects for a total of 100 m² sampling area for each plot (Figure 4). All transects were randomly assigned a compass direction from the center to the outer perimeter of each plot. Belt transects were used to capture the heterogeneity of each habitat type. Plants were identified in the field using *The Guide to Florida Wildflowers* (Taylor 1992).

Netting and colored-pan traps were used to collect a sample of bee diversity in each of the disturbance categories. Methods for capturing bees were guided by a manual for catching and identifying bees by Droege (2010). Blue, white, and yellow painted cups filled with soapy water

were used as pan traps to capture bees in sites once a season in addition to monthly netting sampling. Thirty pan traps per plot were placed in open patches along each of the two transects for 24 hours on days with optimal bee foraging weather (Droege 2010). Bees were identified to species using identification keys from *Bees of the Eastern United States* (Mitchell 1960 and Mitchell 1962).

Results

During the duration of this study, 4,981 bees were collected and identified, representing 48 species and 7,566 plants were identified, representing 81 species. First, sampling effort for both plants and bees was investigated by performing a species area (rarefaction) curve analysis in PCORD 5 (Figure 5 and 6). From those analyses, it was determined whether an appropriate number of species were captured and were therefore representative of the species richness of the communities in this study (Gotelli and Colwell 2001). The results indicate that the methods employed in this study were sufficient for capturing plant and bee species diversity in the study areas.

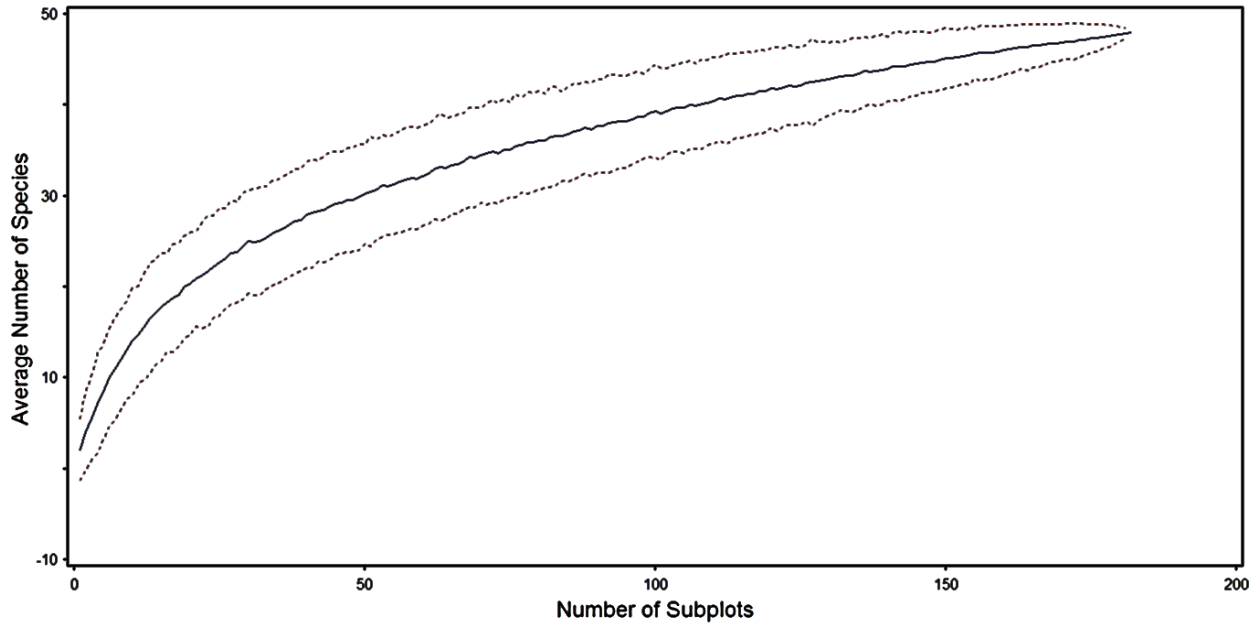


Figure 5. Rarefaction curve for 81 plant species in 192 collections (16 plots x 12 months). Distance measure: Sorensen (Bray-Curtis). First-order jackknife estimate = 101 species. Solid line represents average number of species, dotted lines represent standard error.

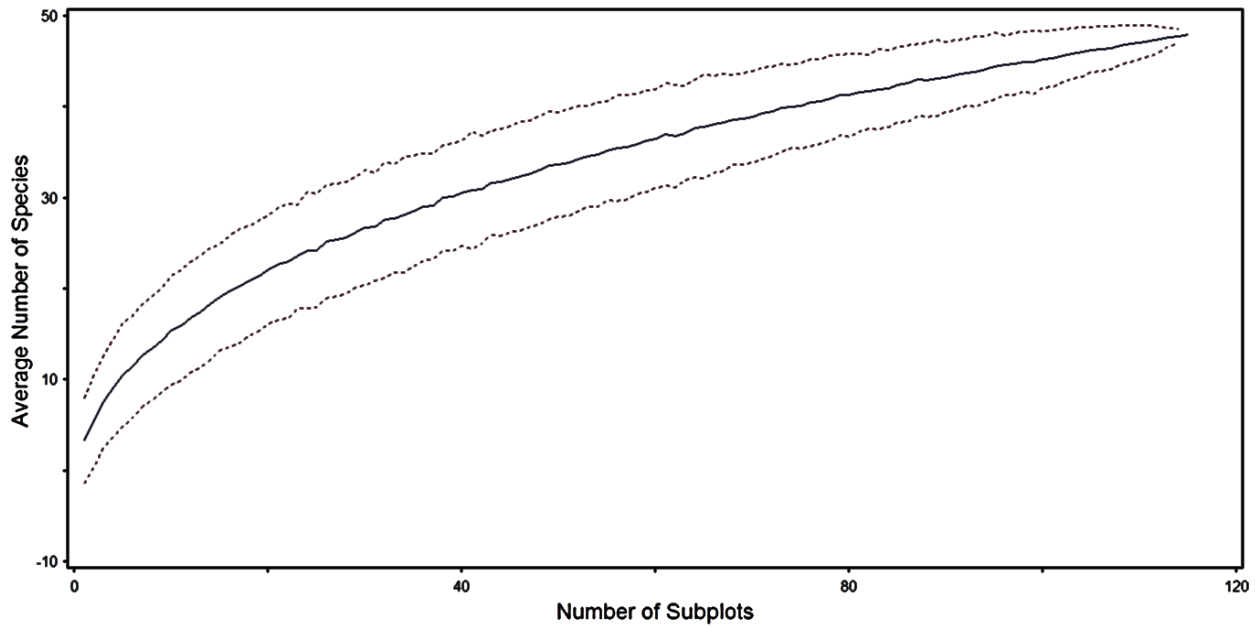


Figure 6. Rarefaction curve for 48 bee species in 192 collections (16 plots x 12 months). Distance measure: Sorensen (Bray-Curtis). First-order jackknife estimate = 67 species. Solid line represents average number of species, dotted lines represent standard error.

Mixed effects modeling in R (3.0.3, R development core team 2013) using the *glmmADMB* package was used to determine whether abundance, richness, and Jost diversity (the number of effective species in a system) of flowering plants and bees across the disturbance levels differed (Fournier et al. 2014) (See Chapter 1 for model details).

Plant abundance, species richness and Jost diversity (effective number of species) were all significantly different across the disturbance levels (Table 2, 3, and 4 and Appendix B1, B2, and B3). Flowering plant abundance, richness and diversity were highest in undisturbed plots followed by heavily disturbed, then moderately disturbed, with pastures having the least plant abundance, richness and diversity. Bee species richness and diversity were not significantly different across disturbance categories (Table 5 and 6). Bee abundance was significantly higher in the undisturbed category ($p=0.016$) and significantly lower in pastures ($p\lll 0.001$) (Table 6 and Appendix B4).

Table 2. Mixed effects coefficients for plant abundance with the best model having only temporal autocorrelation.

	Estimate	Std. error	p	Signif.
Reference	2.9490	0.3070	$\lll 0.001$	***
Moderate	0.4060	0.1953	0.038	*
Heavy	0.9255	0.2006	$\lll 0.001$	***
Pasture	-0.0193	0.2085	0.926	

Table 3. Mixed effects coefficients for plant richness with the best model having both temporal and spatial autocorrelation.

	Estimate	Std. error	p	Signif.
Reference	1.0536	0.1661	$\lll 0.001$	***
Moderate	0.0633	0.1126	0.57	
Heavy	0.5030	0.1024	$\lll 0.001$	***
Pasture	-0.0606	0.1161	0.6	

Table 4. Mixed effects coefficients for plant diversity with the best model having both temporal and spatial autocorrelation.

	Estimate	Std. error	p	Signif.
Reference	0.7141	0.1421	<<<0.001	***
Moderate	0.0393	0.1374	0.7749	
Heavy	0.4141	0.1264	0.0011	**
Pasture	-0.0271	0.1396	0.846	

Table 5. Mixed effects coefficients for bee abundance with the best model having only temporal autocorrelation.

	Estimate	Std. error	p	Signif.
Reference	1.5587	0.6454	0.016	*
Moderate	-0.0579	0.2288	0.8	
Heavy	-0.3351	0.2328	0.15	**
Pasture	-1.0022	0.2371	<<<0.001	***

Table 6. Mixed effects coefficients for bee richness with the best model having both temporal and spatial autocorrelation.

	Estimate	Std. error	p	Signif.
Reference	0.1781	0.3619	0.62	
Moderate	0.0948	0.2463	0.70	
Heavy	-0.0147	0.2536	0.95	
Pasture	-0.236	0.2736	0.39	

Table 7. Mixed effects coefficients for bee diversity with the best model having both temporal and spatial autocorrelation.

	Estimate	Std. error	p	Signif.
Reference	0.195	0.147	0.19	
Moderate	0.048	0.180	0.79	
Heavy	0.164	0.175	0.35	
Pasture	0.031	0.181	0.86	

Change in plant species composition was explored using SigmaPlot 10.0 (Figure 7). There is a clear shift in flowering plant composition with changing habitat disturbance level.

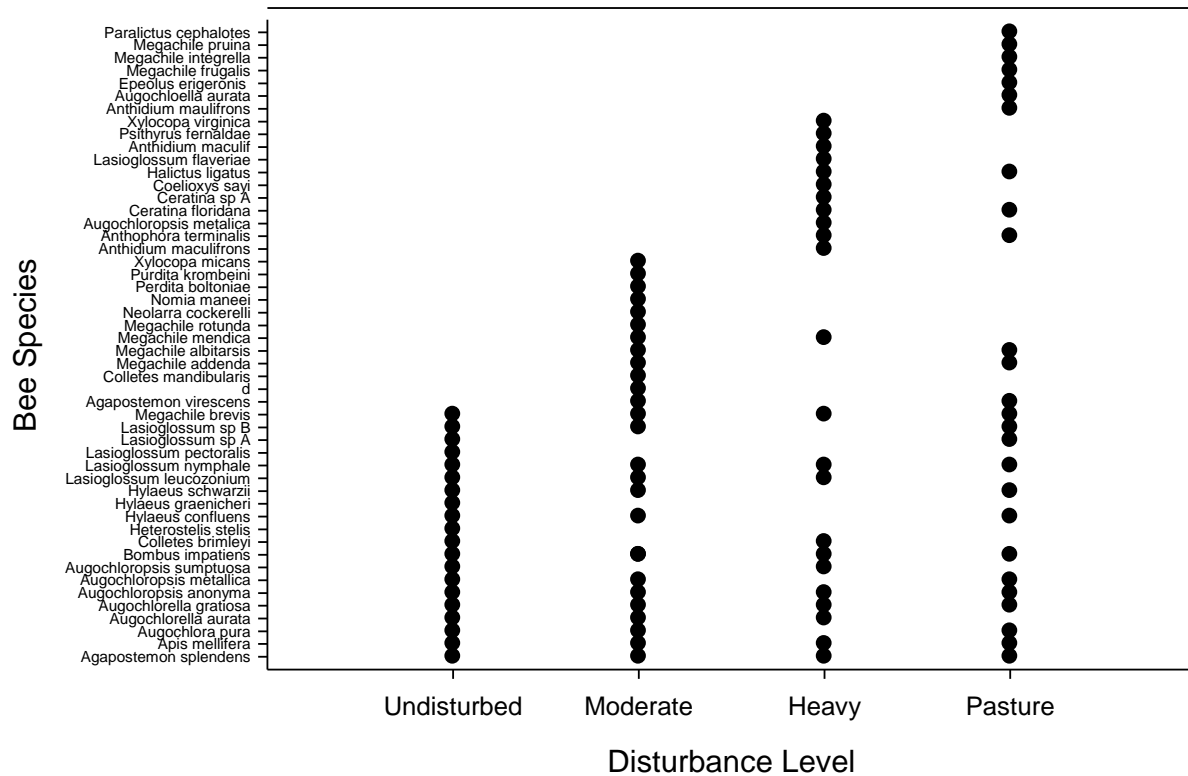


Figure 8. Change in bee species composition across the habitat disturbance levels.

Table 8. Number of endangered, threatened, or non-native plant species found in experimental plots across the disturbance levels.

	Endangered	Threatened	Non-native
Undisturbed	6	1	0
Moderately Disturbed	3	1	0
Heavily Disturbed	3	1	0
Pasture	1	0	5

The accumulated abundance of sampled flowering plants over the course of the year was similar in undisturbed and moderately disturbed areas. Heavily disturbed areas had the highest raw flower abundance, while pastures had the lowest (Appendix C1). Bee abundance was also

compared across the disturbance categories and was shown to decrease with increased levels of disturbance (Appendix C2).

Non-metric multidimensional scaling (NMDS) in PCORD 5 was used to visualize the similarity of bee and plant communities in each of the disturbance categories. Distance between points on the graph relates to their similarity, where greater distances represent less similarity. The plant NMDS revealed overlap in plant community structure of each of the disturbance levels. Undisturbed points were the most spread out in the graph, showing that undisturbed plots were more heterogeneous than the disturbed plots (Figure 9). The results of this ordination suggest that while there is overlap in the plant communities, each disturbance category produces a distinct ellipse, indicating differences in the communities across the habitat disturbance levels. Therefore these plant communities are not the same.

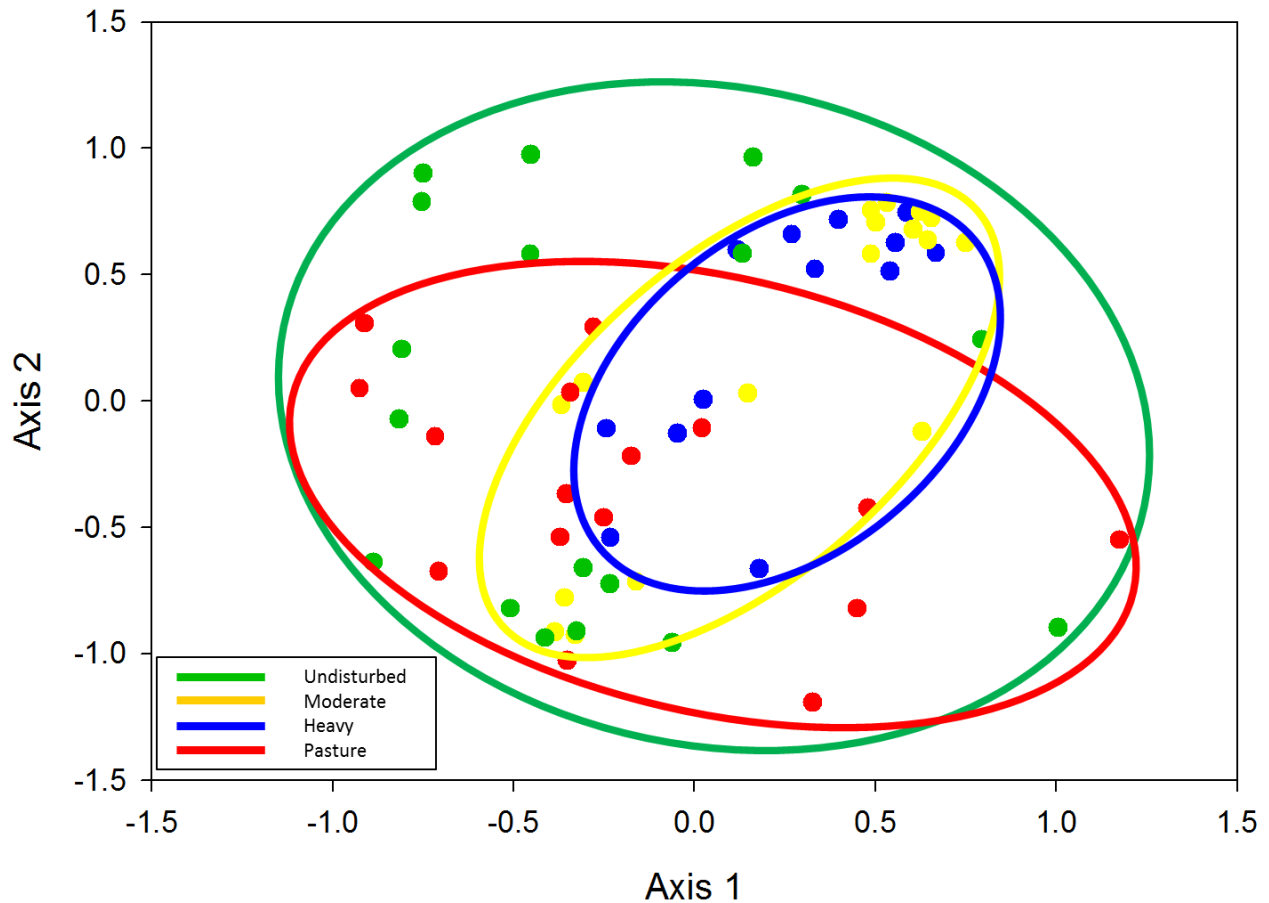


Figure 9. Plant nonmetric multi-dimensional scaling (NMDS) ordination graph of each of the disturbance plots across four seasons with the first two most informative axes based on Bray-Curtis distance. Green ellipse and dots represent the undisturbed plant community, yellow represents moderately disturbed, orange represents heavily disturbed, and red represents pasture.

PCORD 5 was also used to build a distance matrix to numerically determine plant community dissimilarity (Table 9). The undisturbed plant community is least dissimilar from the moderately disturbed community, followed by heavily disturbed, and is most dissimilar from pasture plots.

Table 9. Plant community dissimilarity matrix. Zeroes represent communities that are identical. Numbers greater than zero (>0-1) represent communities that are increasingly dissimilar.

	Undisturbed	Moderate	Heavy	Pasture
Undisturbed	0			
Moderate	0.58	0		
Heavy	0.64	0.27	0	
Pasture	0.86	0.90	0.88	0

The bee NMDS revealed similar overlap in bee community structure across the mechanical disturbance levels as seen in the plant NMDS. Undisturbed points were again the most spread out in the graph, showing that undisturbed plots had a wider variety of bee species composition than the disturbed plots (Figure 10). The results of this ordination also suggest that there is overlap in the bee communities, but each disturbance community produces a distinct ellipse, indicating that bee communities across the habitat disturbance levels are not the same.

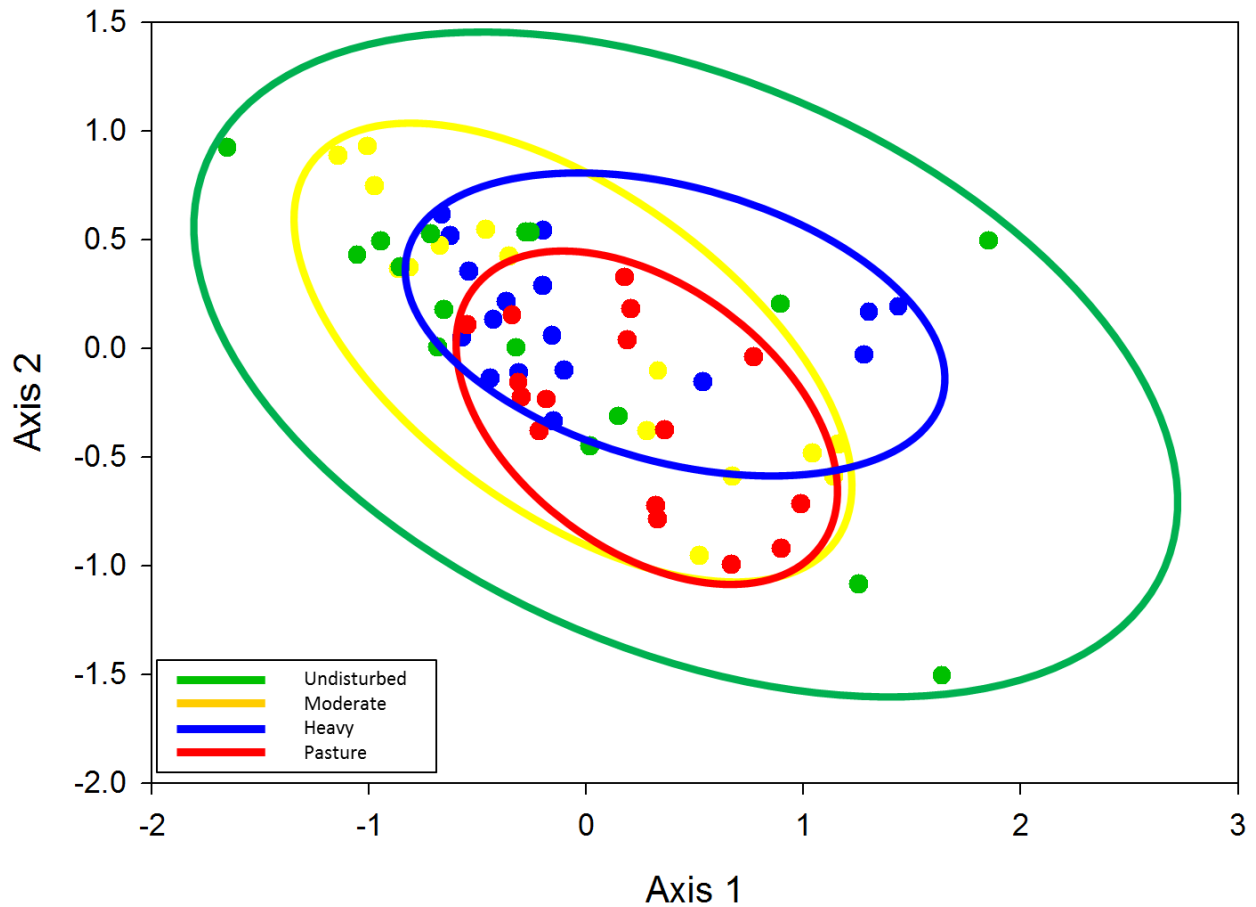


Figure 10. Bee nonmetric multi-dimensional scaling ordination graph of each of the disturbance plots across four seasons with the first two most informative axes based on Bray-Curtis distance. Green ellipse and dots represent the undisturbed bee community, yellow represents moderately disturbed, orange represents heavily disturbed, and red represents pasture.

PCORD 5 was also used to build a distance matrix to numerically determine bee community dissimilarity (Table 10). The undisturbed bee community is least dissimilar from the moderately disturbed community, followed by heavily disturbed, and is most dissimilar from pasture plots.

Table 10. Bee community dissimilarity matrix where zeroes represent communities that are identical, numbers greater than zero (>0-1) represent communities that are increasingly dissimilar.

	Undisturbed	Moderate	Heavy	Pasture
Undisturbed	0			
Moderate	0.18	0		
Heavy	0.32	0.29	0	
Pasture	0.54	0.51	0.33	0

Discussion

The results of this study demonstrate that the plant and bee communities differed across varying intensities of mechanical habitat disturbance. Across the habitat disturbance categories used in this study, there was a significant difference in plant abundance, richness, diversity, and community composition as well as bee abundance and community composition, as predicted (Table 2, 3, 4, 5 and Figure 7 and 8). Flowering plant abundance, richness, and diversity changed significantly with increased habitat disturbance intensity. Bee richness and diversity did not differ with varying levels of disturbance (Table 6 and 7). Although there is a similar bee species richness and diversity across the disturbance levels, bee abundance decreased significantly with increased habitat disturbance intensity (Table 4 and Appendix C2). This observed reduction in the amount of bees with increased disturbance intensity may lead to changes in visitation patterns of bees with available plant species with varying levels of disturbance, which is explored in Chapter 3.

Though bee species richness and diversity did not show a significant change across the disturbance levels, it is clear that the amount and types of available resources (flowering plants) have changed, which may alter bee behavioral foraging choices. If an area is devoid of floral

resources, limited to only a few desirable food sources, or is newly inhabited by an uncommon assemblage of flowering plants, it is not expected to host as many bees, though they may nest in or pass through the area to reach those with more desirable provisions. For example, heavily disturbed and pasture areas, which had the lowest abundance of bees may still be useful to bees as they might use these areas for nesting sites or to facilitate travel between areas with ideal floral options (Grundel et al. 2010). Additional studies to investigate whether bees are using sites across the disturbance levels similarly would be valuable.

The plant and bee communities in this study displayed greater dissimilarity with increased disturbance intensity and are therefore different across the mechanical disturbance levels (Figure 9 and 10, Table 9 and 10). Plant communities were expected to change since sites were mechanically altered, which physically changed those areas through removal or destruction of plants and alteration of soil composition (Menges et al. 2007). Changes in bee species communities may be due to the change in species composition of available flowering plants. Though there are floral resources available, they may not be preferred by bees.

Being mobile organisms, bees are capable of traveling to areas with desirable resources, unlike plants. For example, honey bees will alter their behavior by increasing their flight distance if they fail to gather floral rewards (Waddington 1980). The distance a bee can travel is correlated to body size (Araujo et al. 2004). Larger bees such as honey bees, bumble bees and carpenter bees can travel over 6 km (Osborne et al. 1999, Pasquet et al. 2008). Bumble bees have been observed traveling distances of up to 20 km to reach ideal foraging grounds (Osborne et al. 1999). Smaller bees on the other hand have a reduced foraging range due to smaller body size (Araujo et al. 2004), though most will still travel distances of 150-600 m (Gathmann and Tscharrntke 2002, Zurbuchen et al. 2010). While bee species richness and diversity were similar

across the disturbance levels, it is possible that bee abundance and composition were limited by distances between plots in addition to availability of floral resources. Certain smaller bee species may not have been capable of traveling between experimental plots separated by distances over 150 m unless they were already present within the vicinity of the plots. The smallest bees sampled in this study were found in all four disturbance treatments.

The asymptotic nature of the rarefaction curves (Figure 5 and 6) suggest sufficient sampling effort for both bee and plant species for this study but additional sampling would be ideal to gain a more complete perspective of bee and plant diversity. It is understood from the study performed by Deyrup et al. (2002) that there are over 113 known bee species in the ABS area, but it is important to note that this number reflects collections from any and all habitat types on the property. The flowering plant species found throughout ABS are also well documented and much more numerous than the 81 found, but this study explored only certain habitat types and elevations, limiting the flowering species likely to be found in plots.

This study compared plant and bee species richness, abundance, diversity, and composition with varying levels of mechanical habitat disturbance intensity with the goal of informing the following study (Chapter 3) that will investigate effects of habitat disturbance on interactions between plants and bees. Interactions between plants and visitors are considered a very valuable ecosystem service. Plant-bee interactions depend on a multitude of factors such as availability of resources, plant composition and abundance, and isolation from suitable habitat. This study showed that the availability, abundance and composition of floral resources differed with increased mechanical habitat disturbance. Habitat fragmentation, alteration, and/or destruction have been shown to have negative effects on pollination as seen in many studies (Aizen and Vazquez 1998, Fontaine et al. 2006, Forup et al. 2007, Heithaus and Raymond 1974,

Kearns et al. 1998, Lennartsson 2002, Vanbergen et al. 2013). Habitat change increases the vulnerability of plants and their associated pollinators, weakening the structure and function of the system and increasing the threat of extinction of certain species.

It is important to gain an understanding of how habitat alteration affects those organisms that contribute to plant-visitor networks and the ecosystem service of pollination that often arises from those interactions. It is estimated that the monetary value pollinators provide to the U.S. is \$215 billion a year (Gallai et al. 2009). It is therefore beneficial to understand how changes to available habitat may impact ecological interactions within a system to inform conservation practices that will maintain the continuation of this free service.

Management options include reducing the amount of habitat alteration and performing habitat and resource restoration, appropriately managing existing habitats, reducing herbicide and pesticide use, removal of exotic species and reintroduction of native species. This may guard against declines in plant and pollinator richness and abundance and ensure the continuation of pollination services (Kearns et al. 1998). Future research should encompass the ecology, evolution, population dynamics, and structure of plant-visitor interaction webs in order to gain useful insight for managing suitable habitat.

Habitat loss or alteration is a threat to plant and bee communities as seen in this study and as a result, is expected to impact interactions between plants and bees. Studies pertaining to the effect of habitat alteration on those communities and interactions are necessary. Further studies relating to presence/absence and composition of players within an ecological interaction network will contribute to a more complete understanding of plant-visitor networks and influence conservation planning. This research explored how richness, diversity, abundance, and

composition of flowering plants and bees differed across habitat alteration levels and therefore contributes to the understanding of how anthropogenic disruption of available habitat affects the presence of potential players in a plant-bee network.

CHAPTER 3: STRUCTURE OF PLANT-BEE INTERACTION NETWORKS WITH VARYING LEVELS OF MECHANICAL HABITAT DISTURBANCE

Introduction

Interactions between plants and animals in an ecosystem contribute to global biodiversity (Bascompte and Jordano 2007). These combined interactions form quantifiable networks in which interacting individuals in a system are linked. Most interaction networks contain a multitude of species, many of which overlap in their interactions, and are complex in structure (Bascompte and Jordano 2007). The complexity of these networks contributes to ecosystem diversity, stability, resistance, resilience, and functionality. The tendency of these networks to be complex therefore serves as a vector for biodiversity as well as a way to maintain biodiversity and function within an ecosystem (Bascompte and Jordano 2007).

The greater diversity there is within a system, the more functionally constant and therefore resistant to disturbance an ecosystem will be (Winfree et al. 2007). Ecosystem function and stability depend greatly on the interactions between individuals in a community. Studies have concentrated thus far on the number of links between hosts and their visitors rather than the strength of those interactions. This limits accurate resolution of network patterns (Blüthgen et al. 2007). Understanding how the dynamics of network structure affect these interactions is also limited. Another weakness in the literature is the lack of exploration of most if not all players in a network. Many pollination studies have focused on one or a few plants in a system (Morales and Aizen 2002, Kremen et al. 2002, Winfree et al. 2007), a few associated visitors (Winfree et al. 2007), or a few associated visitors (Kremen et al. 2004, Vazquez et al. 2009, Morandin and Kremen 2012).

Factors that may influence network structure in a plant-visitor web are phenotype, demography, distribution, dispersal ability, and species composition within a community (Vazquez et al. 2009). Alteration to suitable habitat for plants and pollinators is rapidly changing the environment in which plant-bee networks occur normally (Aizen and Vazquez 1998). As a result, the composition, function, and overall performance of plants and pollinators are expected to differ across natural and altered systems (Aizen and Vazquez 1998).

Habitat change and destruction has resulted in alteration of the existing biodiversity on Earth. The consequences of habitat disturbance include change or loss of suitable habitat for plants and their associated visitors. The impact of habitat change on plant-visitor networks is currently uncertain (van der Putten et al 2004, Tylianakis et al. 2007). Fragmented areas are expected to have fewer pollinators present due to lack of resources available for flower visitors, which ultimately impacts plants that rely on pollinator visitation for reproduction (Lennartsson 2002). Anthropogenic habitat disturbance is therefore expected to have an impact on flower visitation choices of potential pollinators. Human-mediated habitat alteration and subsequent biodiversity reduction has the potential to severely impact plant-pollinator interactions and the service of pollination through disruption of network structure (Fontaine et al. 2006). If a plant or pollinator becomes extinct locally due to human-mediated habitat disturbance, or is separated by habitat fragmentation, natural pollination services may be lost for those individuals.

Most flowering plants rely on animal-mediated pollination services for reproduction and gene flow (Hamrick 1982). Plant-visitor interaction networks operate via pollen deposition on the flower by the visitor and the subsequent nectar reward provided in exchange for the pollination service (Heithaus and Raymond 1974). Because of the mutually dependent nature of plant-pollinator interactions, pollination is an important ecosystem service for both natural and

agricultural systems. Plant-visitor interactions often result in seed set for plants which allows the plant to produce fruit (Harris and Johnson 2004). Habitat alteration and subsequent biodiversity reduction has the potential to severely impact plant-visitor interactions and the service of pollination through disruption of network structure (Fontaine et al. 2006). An increased frequency of habitat disturbance has resulted in alteration and/or loss of suitable habitat for plants and pollinators. The impact of habitat fragmentation on plant-pollinator interactions is currently uncertain though fragmented areas are expected to have fewer pollinators present due to lack of resources available for flower visitors, which ultimately impacts those flowers that rely on pollinator visitation for reproduction (Lennartsson 2002). Results from chapter 2 indicate that this is the case in the system chosen for this research.

Mutually-dependent networks such as plant-visitor webs tend to be asymmetrical, heterogeneous, and nested (Vazquez et al. 2009). These networks are asymmetrical in that if a host depends greatly on the visitor, the visitor will depend weakly on the host and vice versa (Bascompte et al. 2006). Past studies have also revealed that plant-visitor interactions are heterogeneous in that most interactions are weakly dependent while only a few are strong (Vazquez et al. 2009). This indicates that plant-visitor interaction webs should have many generalist interactions (with little dependency) and a few specialist interactions (with strong dependency). Bascompte et al. (2006) hypothesized that heterogeneity promotes community coevolution and coexistence and that this will lead to resilience in community structure.

Plant-visitor networks also display a high degree of nestedness (Vazquez et al. 2009). Nestedness occurs when species that interact with only a few individuals (specialists) are subsets of those that interact with many individuals (generalists). Generalized interactions occur when (1) rewards provided by the flower to the visitor are similar among flowers, (2) travel to flowers

is costly, (3) morphological constraints posed by flowers are similar across individuals, and (4) visitor lifespan is greater than the flowering period of the plant (Waser et al. 2012). Though multiple species may be redundantly providing the same service that could be provided by one, redundancy serves as an underlying mechanism for ecosystem stability because each species may be capable of responding differently as the environment changes (Winfree et al. 2007). Nestedness also reduces competition and increases the proportion of individuals that are able to coexist in a system (Bastolla et al. 2009). These tendencies lead to complex network structure in most natural systems.

This study examined the network structure of flowering plants and their associated bee visitors with varying levels of mechanical habitat disturbance over a year to assess how network structure and specificity changed with increased intensity of mechanical habitat disturbance. This research is expected to reveal a change in the composition and interactions of plant-bee networks with increased mechanical habitat disturbance. Plant-visitor interaction studies must strive to understand how the ecology of a system shapes network structure over space and time. Without such consideration, accurate structure and function cannot be determined (Burkle and Alarcón 2011). If the structure of interactions between plants and pollinators change due to human-mediated habitat alteration, this could negatively affect an entire ecosystem.

Methods

To determine the plant-bee network structure in the varying disturbance categories, 16 experimental plots (Chapter 1) were visited in a random order each visit and two randomly assigned transects per plot were scanned for bee-flower visitation (Figure 3 and 4). Plants and

bees were considered generalists (those individuals that interact with more than one species from the other trophic level) or specialists (those individuals that only interact with one species from the other trophic level) based on the number of species with which they were observed to be interacting with. Transects were scanned for visiting bees for 20 minutes using a stop watch. An aerial netting technique was employed to trap bees observed visiting the reproductive flower parts. Once a visitation event was sighted, the stop watch was paused while the bee was caught in an insect net and then placed in a vial denoting the species of plant visited. The timer was then resumed to standardize the time spent scanning among transects (Morandin and Kremen 2012). Surveys were conducted within plot transects once a month for a year to capture seasonal variation.

Results

In this study, a total of 322 bees, representing 31 species were caught visiting 29 species of flowering plants. Data collected in the field were used to create interaction matrices for each disturbance category. Matrices were graphed using the *plotweb* function of the *bipartite* package for R (Dormann et al. 2008, 3.0.3, R development core team 2013), to construct network graphs for each disturbance level (Figure 11, 12, 13, and 14) (See Chapter 1 for more details).

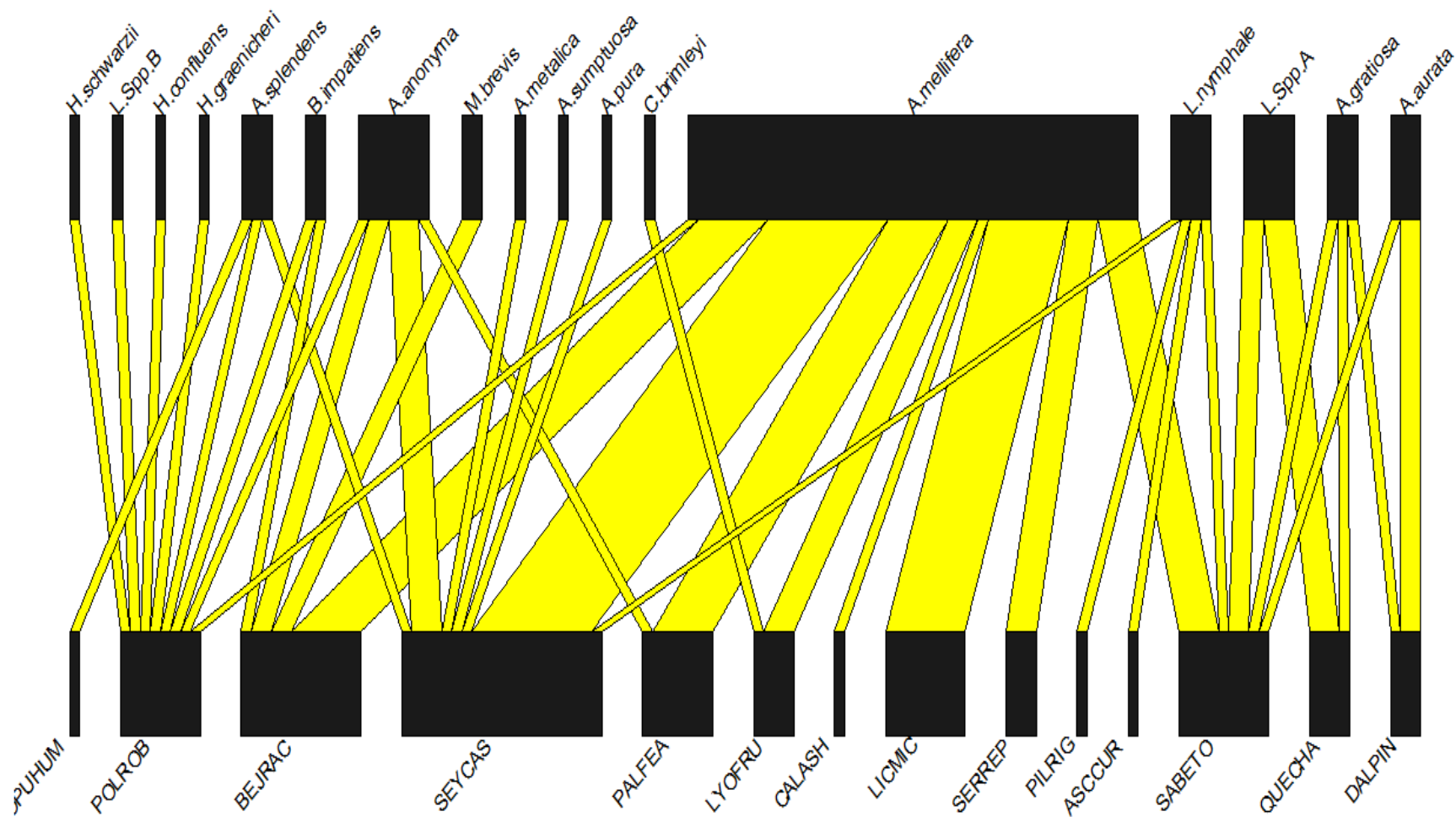


Figure 11. Plant-bee interactions in undisturbed areas of this study (total of 82 interactions). Bee species are on top, plant species are on the bottom. Width of the species and interaction bars is proportional to the sum of interactions.

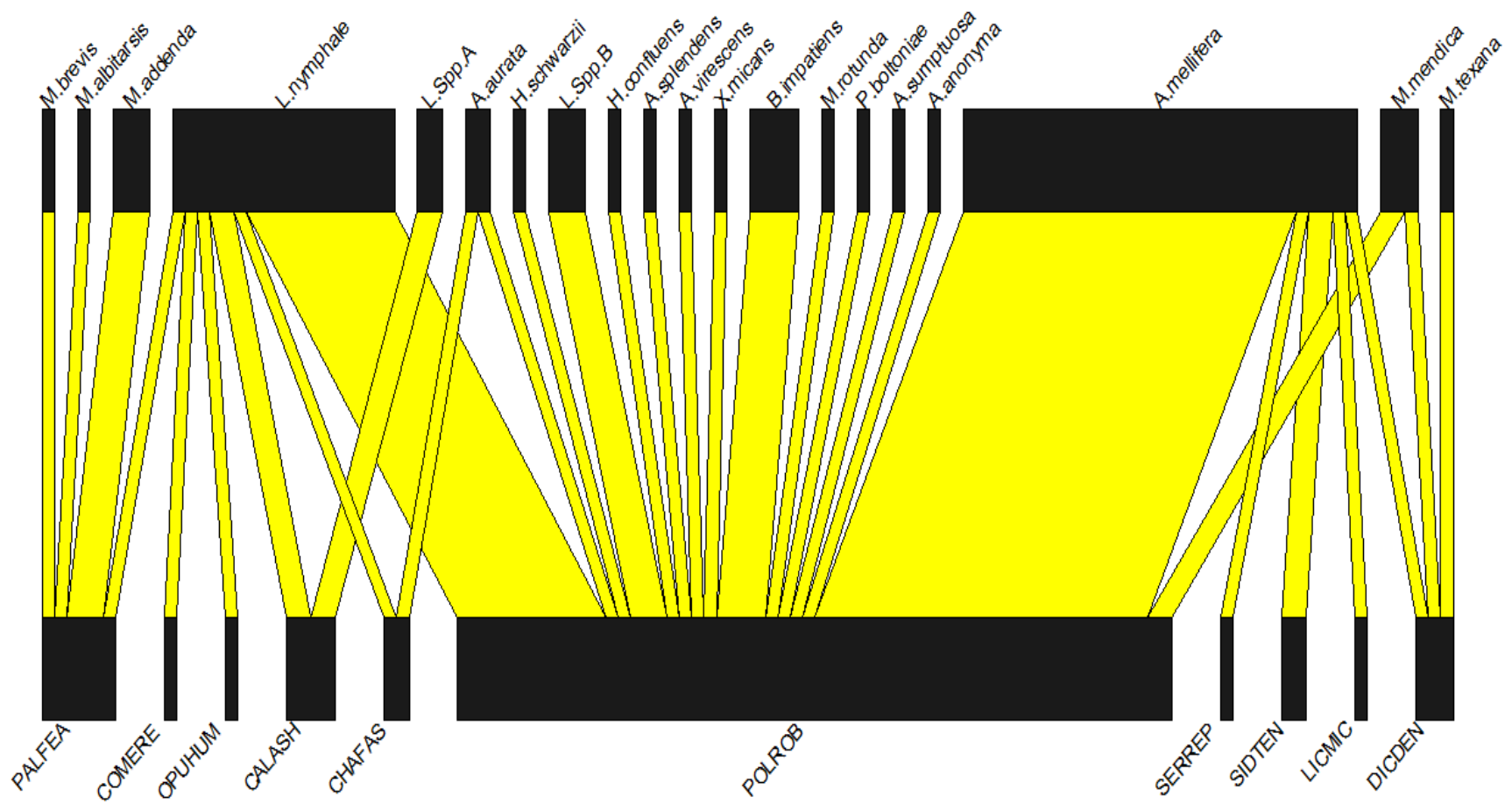


Figure 12. Plant-bee interactions in moderately disturbed areas of this study (total of 78 interactions). Bee species are on top, plant species are on the bottom. Width of the species and interaction bars is proportional to the sum of interactions.

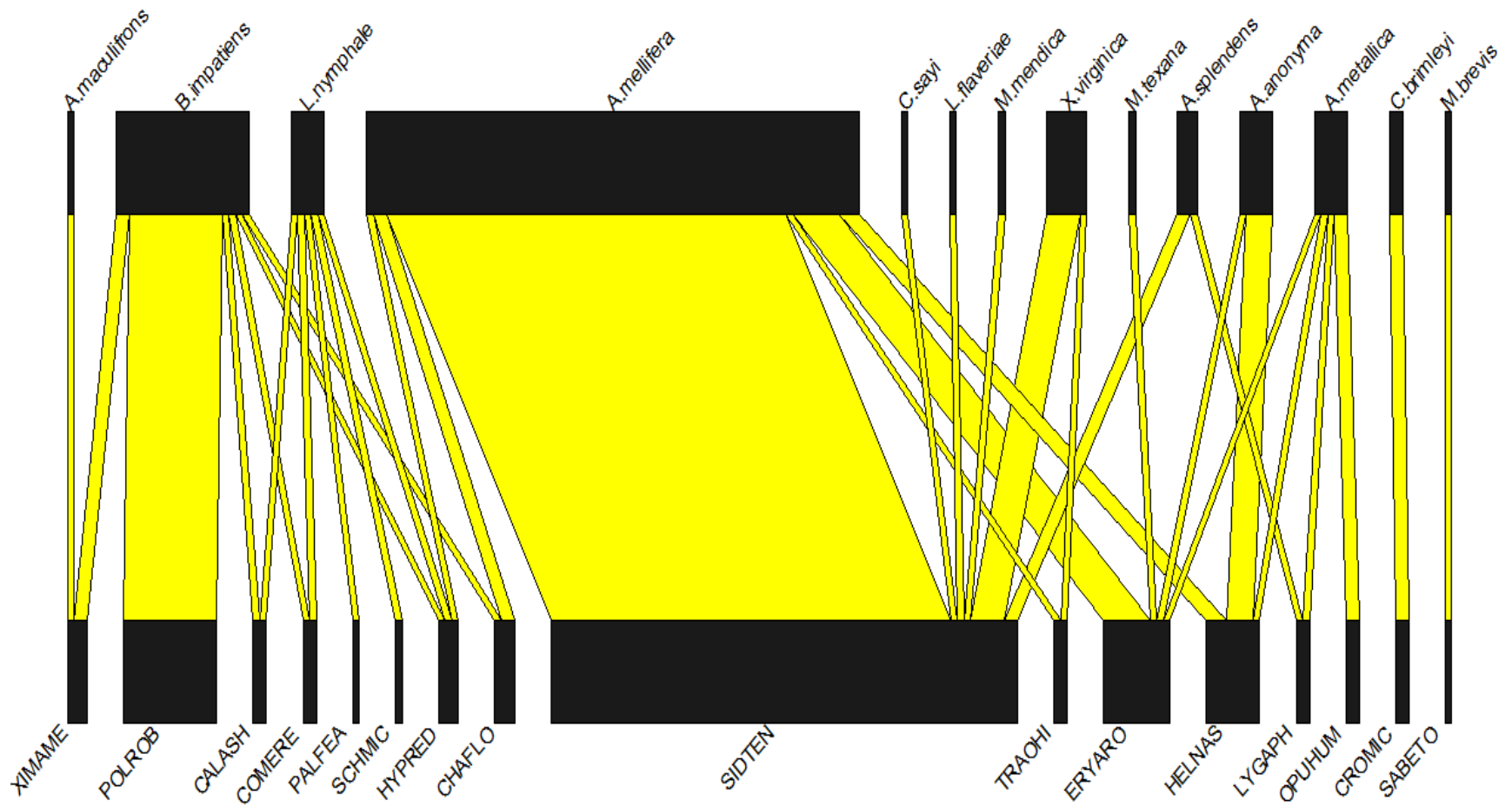


Figure 13. Plant-bee interactions in heavily disturbed areas of this study (total of 126 interactions). Bee species are on top, plant species are on the bottom. Width of the species and interaction bars is proportional to the sum of interactions.

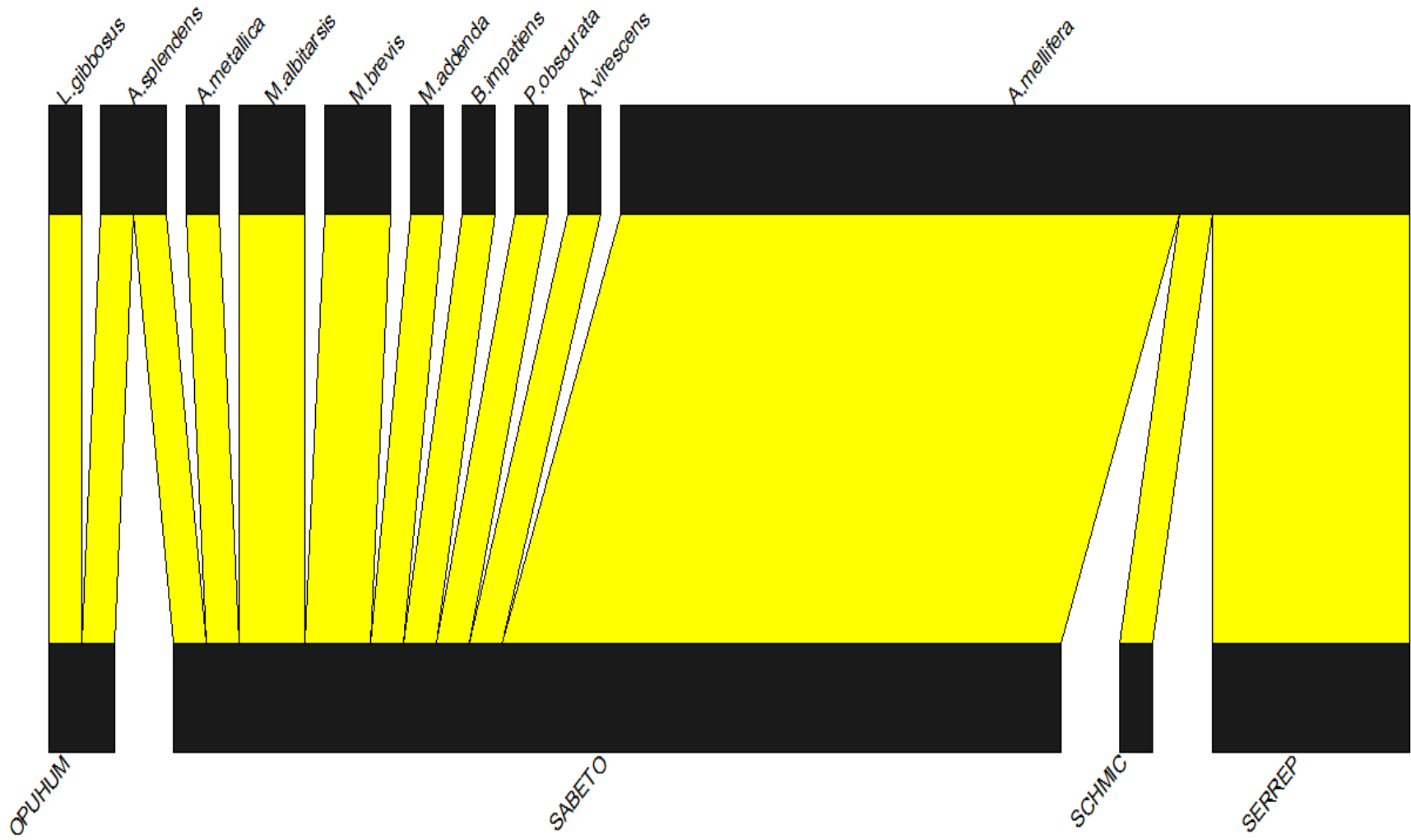


Figure 14. Plant-bee interactions in completely disturbed pasture areas of this study (total of 36 interactions). Bee species are on top, plant species are on the bottom. Width of the species and interaction bars is proportional to the sum of interactions.

Undisturbed and heavily disturbed networks both have more interactions and also have more plant and bee generalists than specialists (Figure 11 and 13, Table 11). Moderately disturbed and pasture networks have fewer interactions and more specialists than generalists (Figure 12 and 14, Table 11). Undisturbed and heavily disturbed networks have the highest number of flowering plant species visited by bees. Moderately disturbed and pasture networks have fewer plant species visited (Table 12). The European Honey Bee (*Apis mellifera*) is the dominant bee species in all four disturbance levels. If *A. mellifera* were removed from each of these networks, a large portion of interactions would be lost (undisturbed – 45% of interactions lost, moderately disturbed – 60%, heavily disturbed – 41%, pasture – 33%).

Table 11. Number of plant and bee specialists and generalists observed in each interaction network across the disturbance levels.

	Plant		Bee	
	Specialists	Generalists	Specialists	Generalists
Undisturbed	6	8	9	8
Moderate	5	4	15	4
Heavy	6	10	7	7
Pasture	2	2	8	2

Table 12. Number of plants and bees caught interacting in each network across the disturbance levels.

	Plants	Bees
Undisturbed	14	17
Moderate	9	19
Heavy	16	14
Pasture	4	10

Matrices were also analyzed using *networklevel* analyses in the *bipartite* package for R (Dormann et al. 2008, 3.0.3, R development core team 2013) to determine and compare the

overall network specialization (Figure 15) and nestedness (Figure 16) as well as interaction strength asymmetry (Figure 17) and robustness to extinction (Figure 18) of each trophic level across the habitat disturbance categories.

Interaction networks from the four disturbance levels were analyzed for network specialization (Figure 15). Network specialization is an index that measures the amount of specialist interactions found in the network from both trophic levels (Dormann et al. 2008). A score of 0 indicates that there is no specialization within a network (all generalist interactions). A score of 1 indicates complete specialization within a network (all species only interact with one species from the opposite trophic level). Network specialization was highest for the heavily disturbed plant-bee network. Undisturbed and moderately disturbed networks were next highest, both with similar specialization scores. The network with lowest network specialization score was the pasture network. Networks were analyzed for network specialization with the honey bee (*Apis mellifera*) removed and showed an increased overall specialization with increased disturbance intensity compared to networks with honey bees included (Appendix C1).

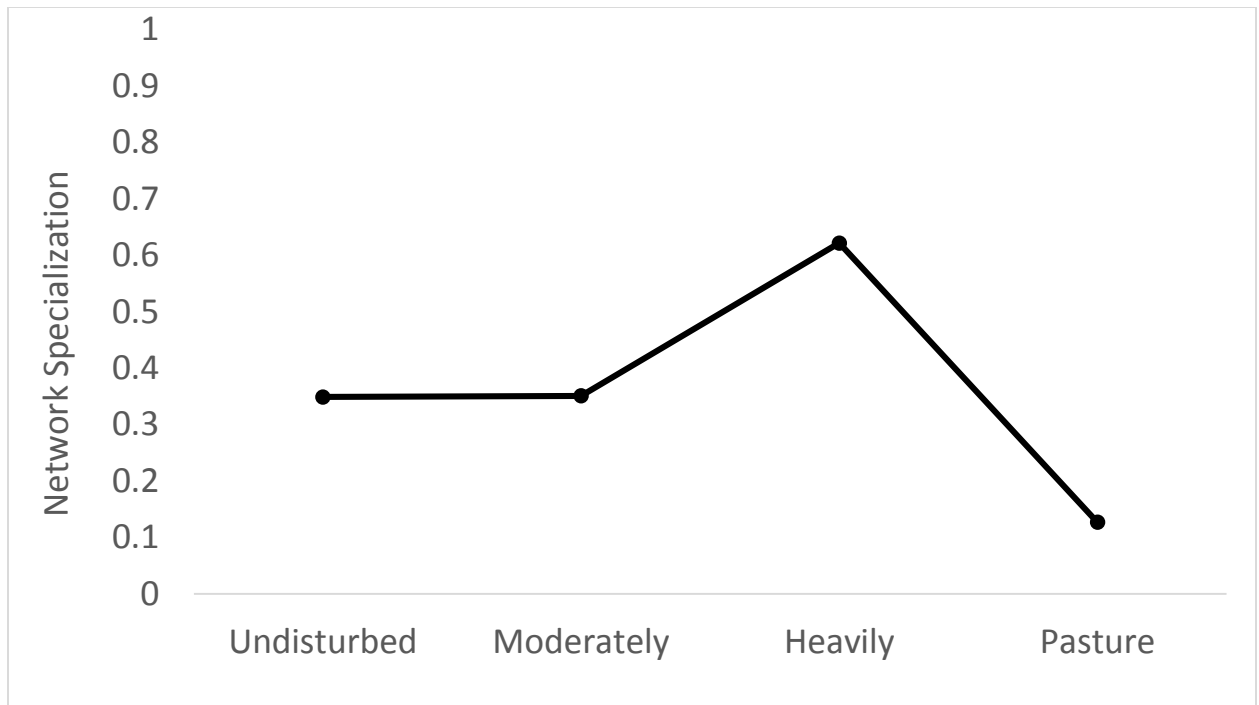


Figure 15. Network specialization scores for each disturbance level. 0= no specialization, 1=complete specialization.

Next, network nestedness was investigated across the disturbance levels (Figure 16). The degree of nestedness represents the proportion of specialist interactions that are nested within the interactions of generalists within a network (Dormann et al. 2008). A network has a high degree of nestedness if more specialist species interactions are subsets of generalist interactions. A network has a low degree of nestedness the less nested interactions are. Moderately disturbed and pasture networks displayed the highest degree of nestedness because they had the highest proportion of specialists for both trophic levels and those specialists interacted with generalists from the opposite trophic level, resulting in a highly nested arrangement of interactions (Table 11). Undisturbed and heavily disturbed networks had less nestedness as a result of having more generalist plants and bees and fewer nested interactions between specialists and generalists. Networks were analyzed for nestedness with the honey bee

(*Apis mellifera*) removed and showed decreased nestedness in undisturbed, heavily disturbed and pasture networks compared to networks with honey bees included (Appendix C2).



Figure 16. Graph showing nestedness of plant-bee networks across the disturbance levels. Nestedness measure considers interaction frequencies. 1=perfect nestedness, 0=perfect chaos.

Interaction strength asymmetry (dependence) was also compared across the disturbance categories (Figure 17). This measure indicates the strength of dependence bees and plants have on each other (Dormann et al. 2008). For example, due to the heterogeneous nature of plant-bee interactions, if a plant depends strongly on the interaction with a bee visitor, the bee visitor likely depends weakly on the interaction with the plant (Bascompte et al. 2006). In moderately disturbed and pasture networks, positive dependence scores suggest that bees relied more heavily on interactions with the plants they visited than the plants depended on bees. In undisturbed and heavily disturbed networks, negative dependence scores suggest plants relied more heavily on interactions with the bees that visited them than bees depended on plants. Networks were

analyzed for dependence with *Apis mellifera* removed and showed increased dependence scores in moderately disturbed, heavily disturbed and pasture networks compared to networks with honey bees included indicating bees would be even more dependent on plants if honey bees were missing from the network (Appendix C3).



Figure 17. Interaction strength asymmetry (dependence) graphs. Positive numbers indicate higher bee dependence on plants, negative numbers indicate plant dependence on bees.

Plant and bee robustness to extinction was also explored using *Networklevel* analysis (Figure 18). This measure evaluates the likelihood of species survival if a large portion of the opposite trophic level is removed (Dormann et al. 2008). A robustness score of 1 suggests that the extinction curve decreases mildly (very robust) with species losses. In other words, most species would survive in the network if a large fraction of the other trophic level is eliminated. A robustness score of 0 suggests that the extinction curve decreases abruptly (not robust). If a small amount of species in the network are lost, most other trophic level species would go extinct. For

example, if a plant that is visited by many bee species no longer receives visits from some of those bee species, it will likely still survive due to interactions from other visitors. On the other hand, if a plant is only ever visited by one species of bee and that bee species goes extinct, the plant has a high probability of extinction due to the lack of visitation and subsequent pollination service. Plants and bees in undisturbed and heavily disturbed habitats displayed the highest robustness to extinction since there were more generalists in those areas. Moderately disturbed and pasture plants and bees had lower robustness scores. Despite these patterns, both trophic levels (plants and bees) in all four disturbance categories had robustness scores above 0.50, indicating that most species would survive if some extinctions occurred.

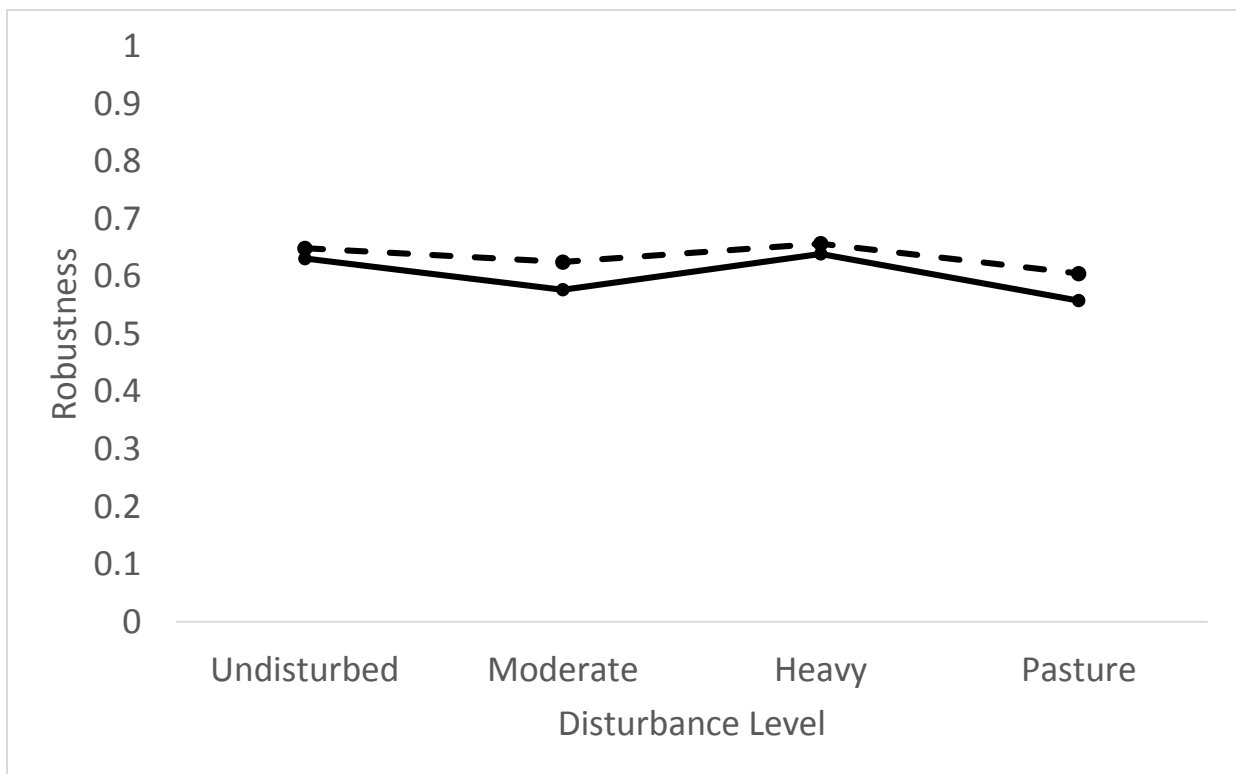


Figure 18. Plant and bee robustness to extinction as habitat disturbance intensity increases. Dashed line represents plant robustness scores and solid line represents bee robustness scores.

Understanding the limitations of network indices (Chapter 1), an ordination technique was used to further investigate the similarity of these interaction matrices in PCORD 5. Non-metric multidimensional scaling (NMDS) was used to summarize and compare interaction data in an ordination graph which places similar samples in close proximity, and dissimilar samples further away in space (Gotelli and Ellison 2004) (Figure 19). Table 13 summarizes the stress of the iterations performed in this analysis. The results of this ordination suggest that while there is overlap in the structure of the interaction networks, each network matrix produces a distinct ellipse, thereby indicating that across habitat disturbance levels, these plant-bee networks are not the same.

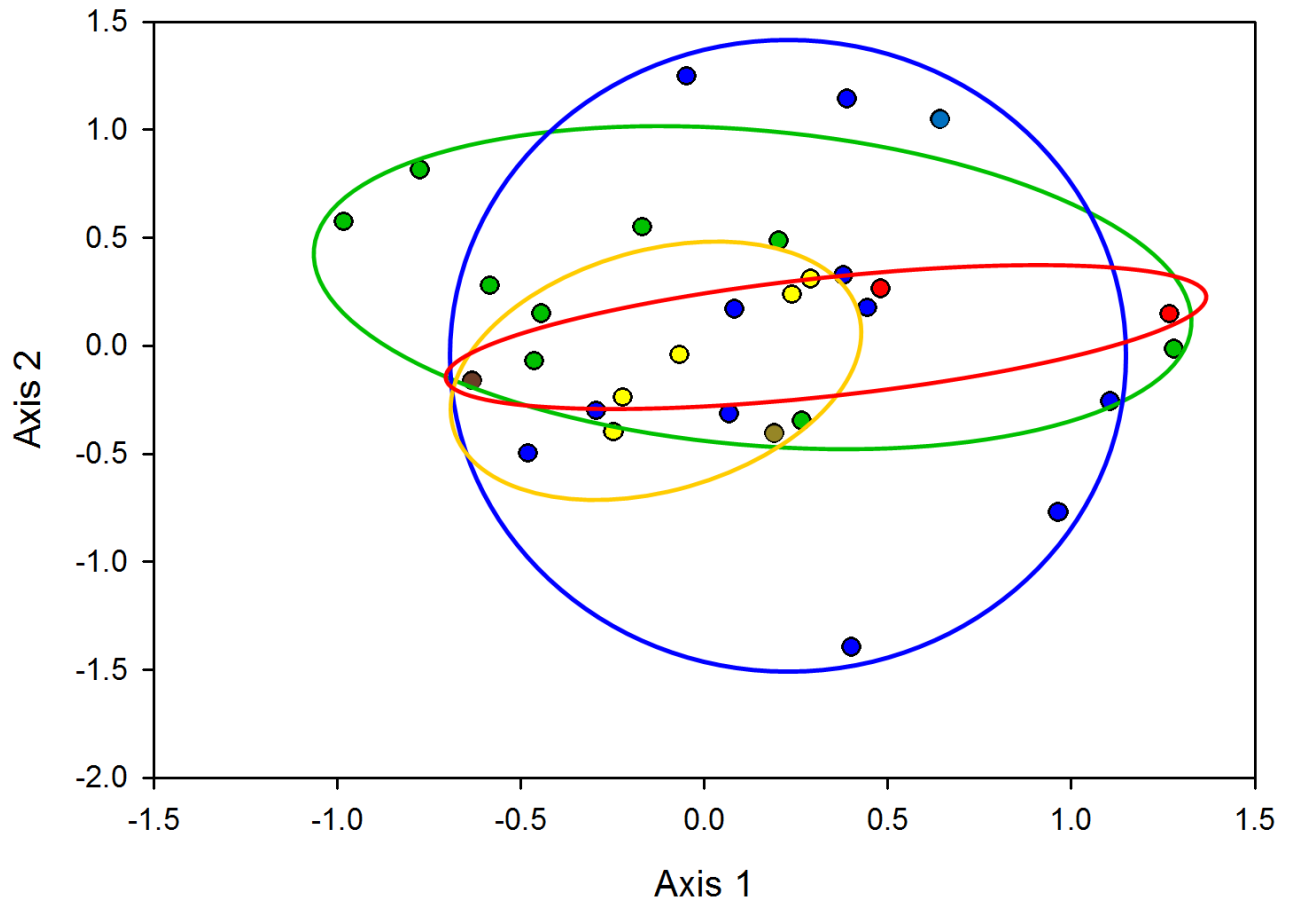


Figure 19. Nonmetric multi-dimensional scaling ordination graph showing first two most informative axes analyzing plant-bee interactions across the disturbance levels. Green ellipse represents the undisturbed plant community, yellow represents moderately disturbed, orange represents heavily disturbed, and red represents pasture interactions.

Table 13. Stress of nonmetric multi-dimensional scaling ordination analysis in relation to number of axes.

STRESS IN RELATION TO DIMENSIONALITY (Number of Axes)

Axes	Stress in real data 10 run(s)			Stress in randomized data Monte Carlo test, 20 runs			
	Minimum	Mean	Maximum	Minimum	Mean	Maximum	p
1	41.428	50.155	57.640	45.655	51.965	56.887	0.0476
2	22.715	25.893	40.146	25.732	29.980	40.132	0.0476

p = proportion of randomized runs with stress < or = observed stress
i.e., $p = (1 + \text{no. permutations} \leq \text{observed}) / (1 + \text{no. permutations})$

PCORD 5 was also used to build a distance matrix to numerically determine interaction network dissimilarity (Table 14). The undisturbed network is least dissimilar from the moderately disturbed community, followed by heavily disturbed, and is most dissimilar from pasture plots.

Table 14. Plant-bee interaction network dissimilarity matrix across the disturbance levels. Zeroes represent interaction networks that are identical. Numbers greater than zero (>0-1) represent networks that are increasingly dissimilar.

	Undisturbed	Moderate	Heavy	Pasture
Undisturbed	0			
Moderate	0.40	0		
Heavy	0.49	0.51	0	
Pasture	0.69	0.60	0.68	0

From chapter 2, we saw that plant species composition changed across the mechanical habitat disturbance levels. Knowing this, the plant species composition of those plants that were actually visited by bees was explored using SigmaPlot 10.0 (Figure 20). There was a shift in visited flowering plant composition with changing habitat disturbance level. As habitat

disturbance intensity increased from undisturbed to pasture sites, the assemblage of plant species being visited by bees changed. Heavily disturbed plots had the greatest number of flowering plant species visited, while pastures had the least. During the sampling periods, there were no instances of invasive plant species being visited by bees. There was also a shift in bee species found visiting flowering plants (Figure 21) across the disturbance levels.

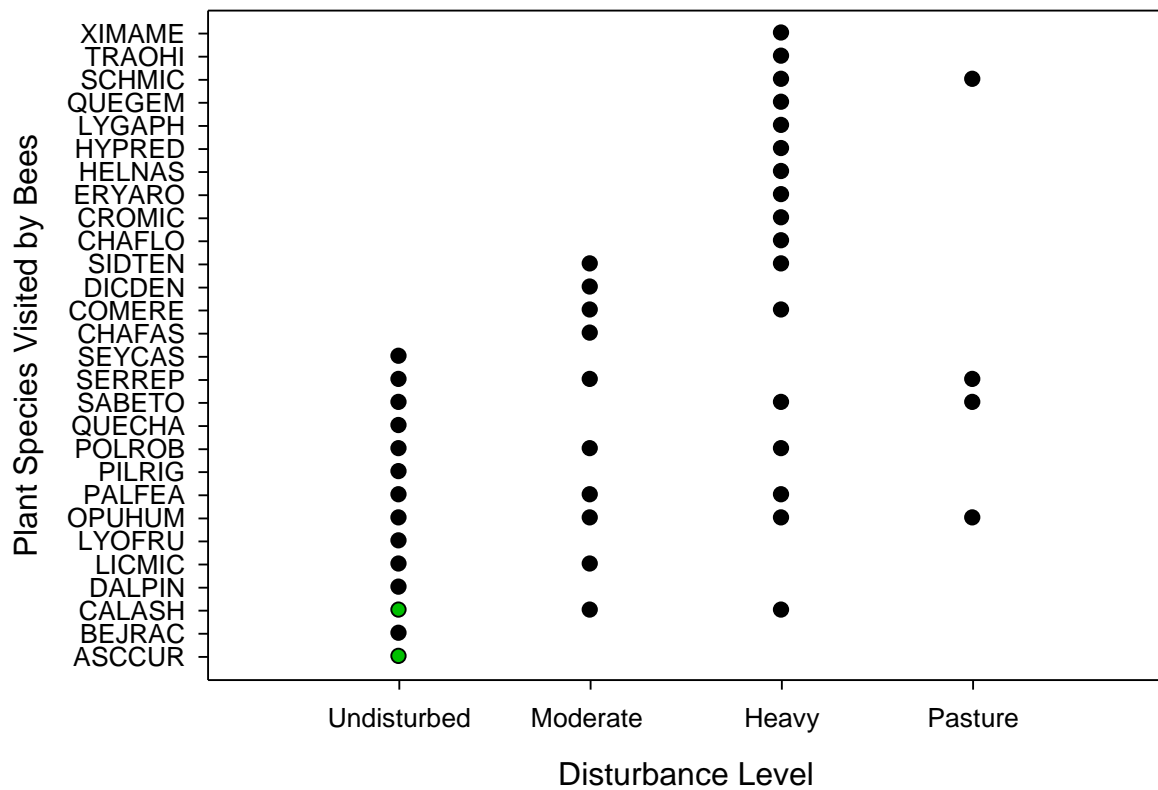


Figure 20. Graph showing change in composition of plant species visited by bees across the disturbance levels. Green dots represent plant species of concern (endangered or threatened).

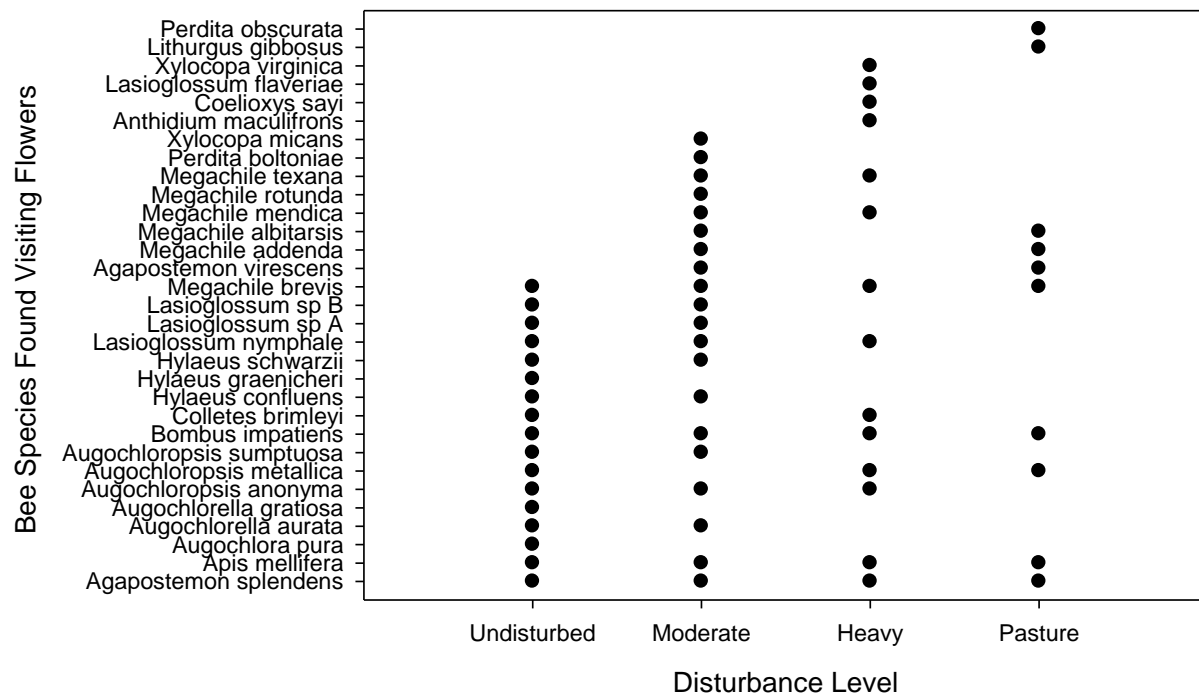


Figure 21. Graph showing change in composition of bee species found interacting with flowers across the disturbance levels.

Discussion

Plant-bee interactions changed with increased mechanical disturbance intensity, as demonstrated by the results of this study. Undisturbed and heavily disturbed networks had the most interactions with the heavily disturbed networks having the greatest. (Undisturbed: 82 total plant-bee interactions, heavily disturbed: 126). The moderately disturbed network had 78 total plant-bee interactions and the pasture network had 36 total interactions. Network specialization, nestedness, plant and bee dependence, and robustness to extinction differed across the disturbance levels (Figure 15, 16, 17, and 18). The results of the NMDS ordination and dissimilarity matrix suggest that the networks from the four disturbance categories shared some

similarities but each network was distinct, becoming more dissimilar with increased disturbance intensity (Figure 19 and Table 14). From this, it is clear that the plant-bee networks observed in this study were different with varying levels of mechanical habitat disturbance intensity. If the European Honey Bees (*Apis mellifera*) were removed from each of these networks, a large portion of interactions would be lost. The network specialization, nestedness, and dependence scores change when honey bee interactions are removed from the network, indicating that honey bees are not only the dominant plant-visitor in each of these networks, but they also contribute largely to network structure and interactions (Appendix D1, D2, and D3).

The assemblage of plant species visited by bees and the assemblage of bee species caught visiting flowers also changed with increased mechanical habitat disturbance intensity (Figure 20 and 21). These patterns were likely driven by changes in bee foraging behavior due to changes in overall plant species composition (Chapter 2). If an area is devoid of floral resources or limited to only a few desirable food sources, it is not expected to host as many bee visitors, though they may nest in or pass through the area to reach those with more desirable resources. For example, pasture areas, which had the least diverse plant-bee interaction network may still be useful to bees as they may be using these areas for nesting sites or to facilitate travel between areas with ideal floral options (Figure 14).

The ecosystem service of plant pollination is extremely valuable to ecosystem function and resilience (Kremen et al. 2007). Further research is necessary to understand the influence of plant visitation on ecosystem structure, species evolution, and conservation. With growing human population and development, anthropogenic disturbance is an unavoidable threat to delicate ecological interactions such as plant-visitor interactions within an ecosystem (Vanbergen et al. 2013). Archbold Biological Station is nested within a human-modified landscape that

largely consists of agricultural land such as orange groves. Preserving natural areas such as ABS and the pollinators that are currently present there may benefit surrounding crop fields by providing a source of pollinators.

It is estimated that pollinators provide services to the U.S. worth \$215 billion a year (Gallai et al. 2009). It is only realistic to assume that humans will continue to alter ecosystems as we further expand our species, but conserving valuable ecosystem services such as crop pollination is necessary. It therefore benefits humans to practice informed land-use change to ensure the continuation of this free service.

CHAPTER 4: CONCLUSIONS

Highly diverse systems have been shown to be more functionally constant and resistant to disturbance (Winfree et al. 2007). The continued function and stability of an ecosystem depends greatly on the strength of interactions between individuals in a community. The stability of interaction networks therefore contributes to an ecosystem's response to change. As landscapes continue to undergo human-mediated alteration, ecological interaction networks such as plant-visitor webs may be threatened and it is therefore prudent to investigate the effects of anthropogenic habitat change on such interactions (Fortuna and Bascompte 2006). As a result of alteration or loss of available habitat for individuals to live in, the risk of species extinction rises with increased habitat alteration (Fortuna and Bascompte 2006). Interactions between remaining individuals may also decline with increased destruction levels due to changes in composition of plant and bee species, with the threat of network-collapse at threshold levels of habitat-loss (Fortuna and Bascompte 2006).

This research explored changes in plant-bee networks with increased intensity of human-mediated habitat alteration. It contributes to the understanding of anthropogenic disruption of habitat and its effects on the presence, composition and interactions of players in a plant-visitor mutualistic network. Results revealed changes in the composition and structure of plant-bee networks in a system that has undergone mechanical habitat change. The abundance, richness and diversity of flowering plants were all highest in undisturbed areas as expected and the composition of flowering plants present in research plots differed across disturbance levels. Bee abundance was also highest in undisturbed areas and there was a shift in bee species composition as well. Changes in the amount and types of flowering plants present across disturbance levels may drive changes in bee abundance and composition because if floral resources for bees differs,

this may influence bee foraging behavior and presence. Mechanical habitat change had an impact on plant and bee communities and the interactions between them as seen in this study. This research specifically explored how flowering plant and bee species richness, diversity, abundance, and composition as well as interactions between plants and bees changed across mechanical habitat alteration levels. As the intensity of habitat disturbance increased, there were changes in plant abundance, richness, diversity, and community composition as well as bee abundance and community composition (Chapter 2). Bee richness and diversity did not differ with varying levels of disturbance. The interactions between flowering plants and bees also changed across the mechanical disturbance categories. Network specialization, nestedness, interaction strength asymmetry, and robustness to extinction differed with varying levels of mechanical habitat disturbance (Chapter 3).

The abundance of bees found in this study decreased significantly with increased mechanical disturbance intensity (Chapter 2). It was also found that bees do not interact similarly with available flowering plant species across the disturbance levels (Chapter 3). Change in the amount and types of available resources (flowering plants) may have contributed to changes in the foraging habits and therefore presence or absence of bees. If resources in an area are limited to only a few desirable food sources, the area is not expected to host as many bees, though it is possible that they may use those areas for nesting or passing through to reach areas with ideal floral sources.

The impacts of mechanical habitat change on both diversity of and interactions between plants and bees in this study are expected to influence the foraging behavior of bees, which may increase the vulnerability of both plants and bee-visitors, weakening the structure and functioning of the system and increasing the threat of extinction of certain species (Aizen and

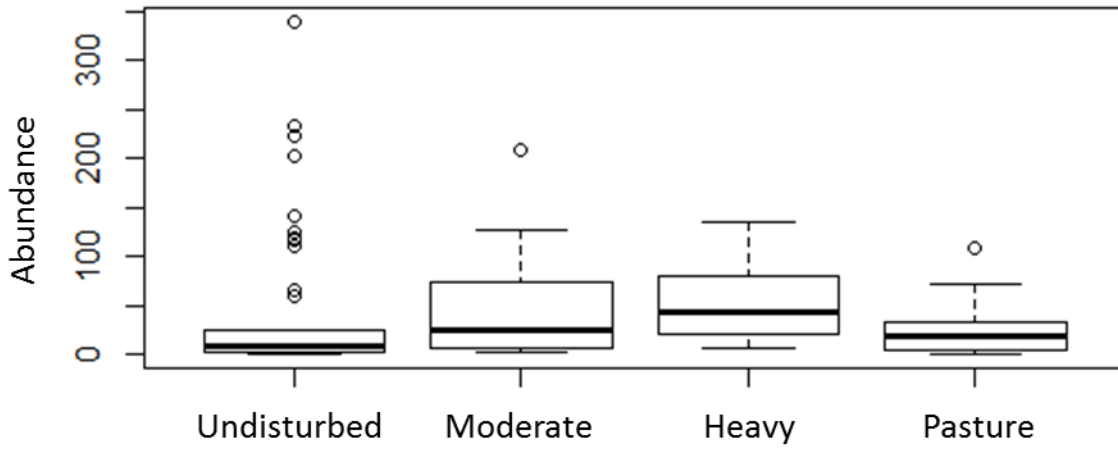
Vazquez 1998, Fontaine et al. 2006, Forup et al. 2007, Heithaus and Raymond 1974, Kearns et al. 1998, Lennartsson 2002, Vanbergen et al. 2013). Ultimately, the composition, structure and function of ecological interaction networks facilitate biodiversity in a system. The ecological factors that support interaction networks must be maintained in order to preserve biodiversity, stability and function of ecosystems as a whole. Anthropogenic habitat loss is a major threat to plant-animal interactions and more studies investigating the effects of human-mediated habitat alteration and destruction on those interactions are necessary. Research relating to the response of plant-visitor networks to habitat change will contribute to a more complete understanding of plant-visitor interactions and the vulnerability of these networks to change. Some management options based on the findings of this research include conservation and restoration of native flowering plants, which is likely to promote bee presence and abundance as well as performing informed land-use change to avoid reaching threshold levels of habitat alteration that may lead to network collapse. By doing so, management and conservation efforts may help maintain plant-visitor interactions and guard against loss of ecosystem function.

APPENDIX A: SITE LOCATIONS

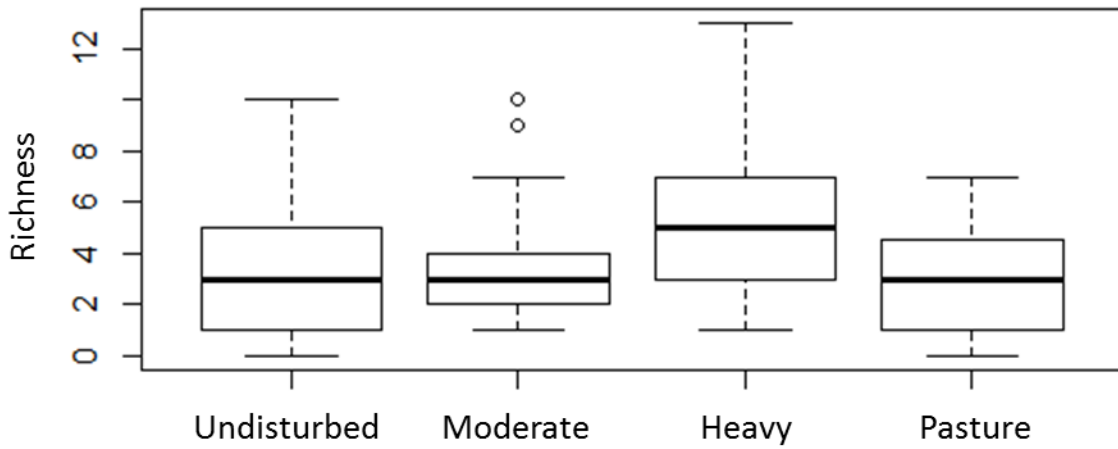
Appendix A. Site locations for experimental plots in the McJunkin Tract, Lake Wales Ridge Wildlife and Environmental Area, Florida Fish and Wildlife Conservation Commission, Archbold Reserve, Archbold Biological Station (Menges et al. 2007).

PLOT #	Location	Habitat Type	Northing	Easting
1	FFWCC WEA	Heavily Disturbed	3008645	462925
4	FFWCC WEA	Heavily Disturbed	3008058	463430
5	FFWCC WEA	Heavily Disturbed	3008163	462919
7	FFWCC WEA	Heavily Disturbed	3008464	462743
8	Reserve Pasture	Pasture	3004599	463660
9	Reserve Pasture	Pasture	3004504	463627
10	Reserve Pasture	Pasture	3004108	463618
14	Reserve Pasture	Pasture	3001775	463637
15	Reserve SE Scrub	Moderately Disturbed	3000345	463605
16	Reserve SE Scrub	Moderately Disturbed	3000670	463490
17	Reserve SE Scrub	Moderately Disturbed	3000656	463228
20	Reserve SE Scrub	Moderately Disturbed	3001670	463277
23	ABS Reference Site	Undisturbed Scrub	3000870	463851
24	ABS Reference Site	Undisturbed Scrub	3002036	463948
27	ABS Reference Site	Undisturbed Scrub	3005351	464023
28	ABS Reference Site	Undisturbed Scrub	3003827	463910

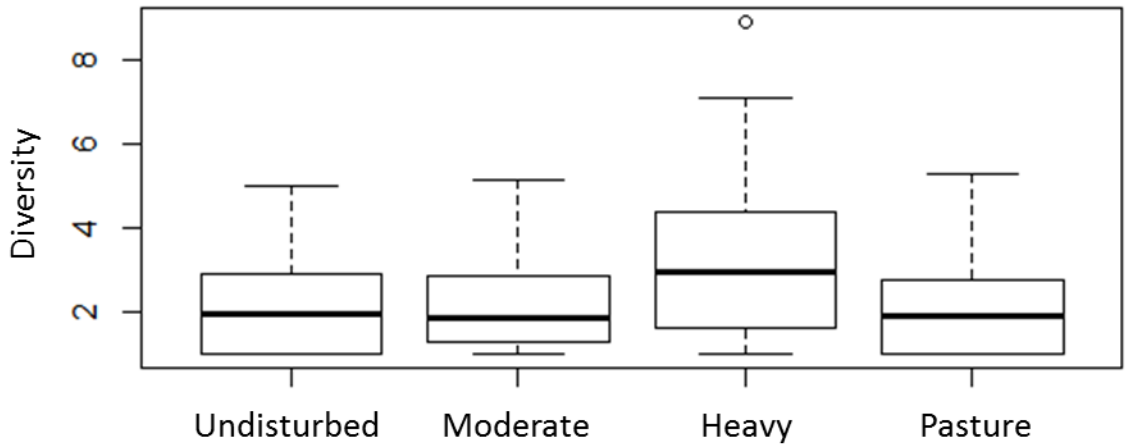
**APPENDIX B: ABUNDANCE, RICHNESS AND DIVERSITY BOXPLOTS
FOR DIVERSITY MEASURES WITH A SIGNIFICANT EFFECT**



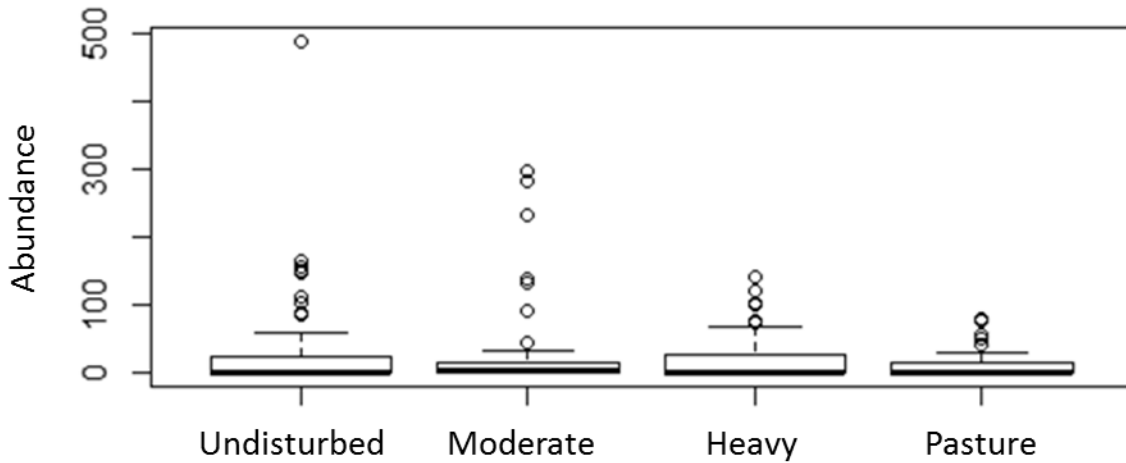
Appendix B 1. Plant abundance box plot with raw values (not considering effects of temporal or spatial autocorrelation).



Appendix B 2. Plant richness box plot with raw values (not considering effects of temporal or spatial autocorrelation).

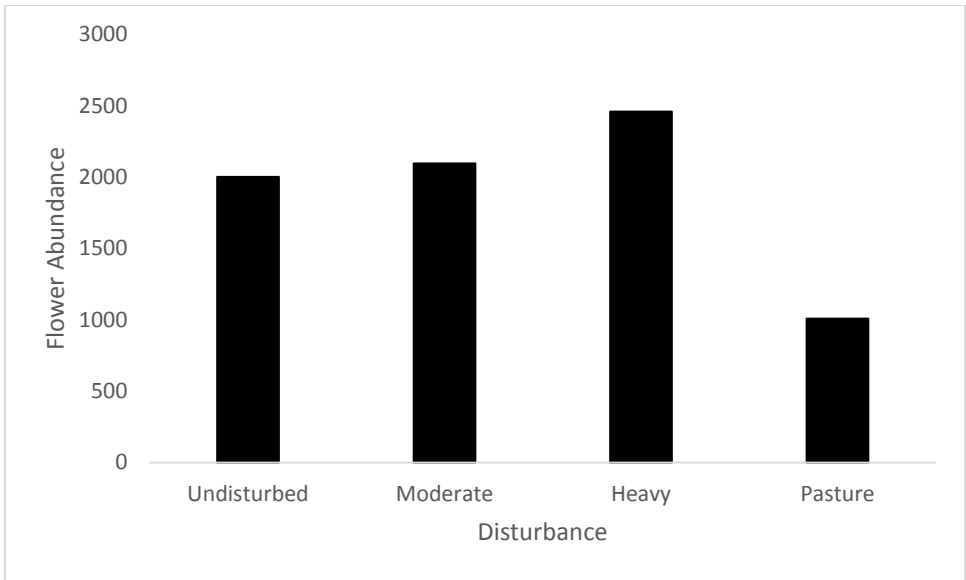


Appendix B 3. Plant diversity box plot with raw values (not considering effects of temporal or spatial autocorrelation).

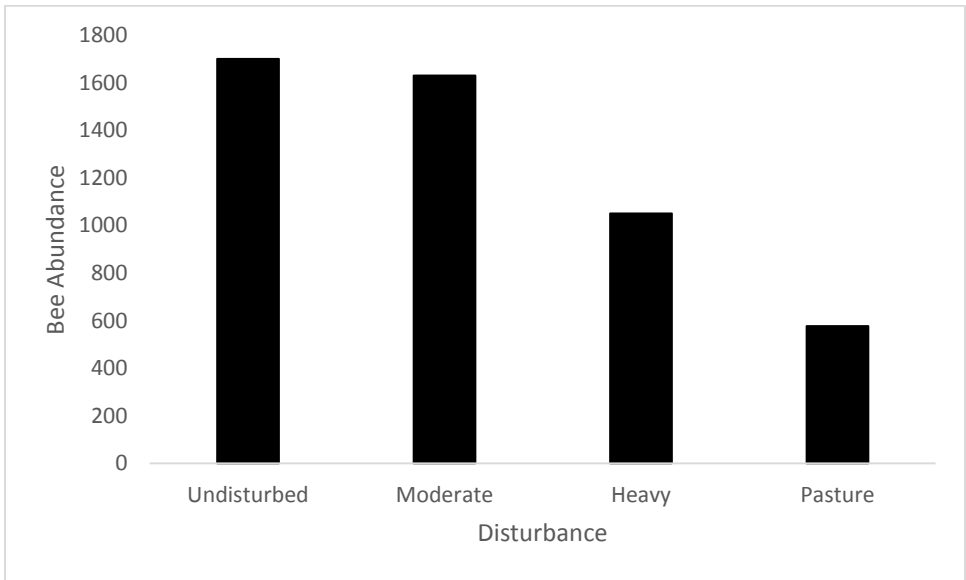


Appendix B 4. Bee abundance box plot with raw values (not considering effects of temporal or spatial autocorrelation).

APPENDIX C: PLANT AND BEE ABUNDANCES



Appendix C 1. Accumulated abundance of flowering plants (and therefore potential floral resources for bees) found in each disturbance level over the course of a year. Note: This does not reflect the abundance of flowers blooming at one time.

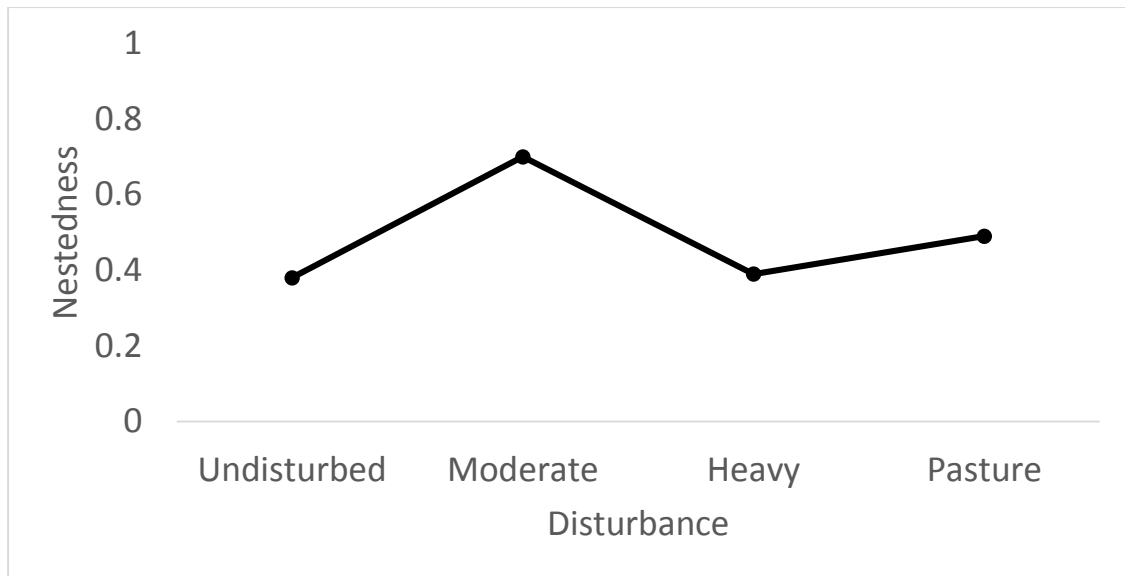


Appendix C 2. Accumulated abundance of bees found in each disturbance level over the course of a year. Note: This does not reflect the abundance of bees present at one time.

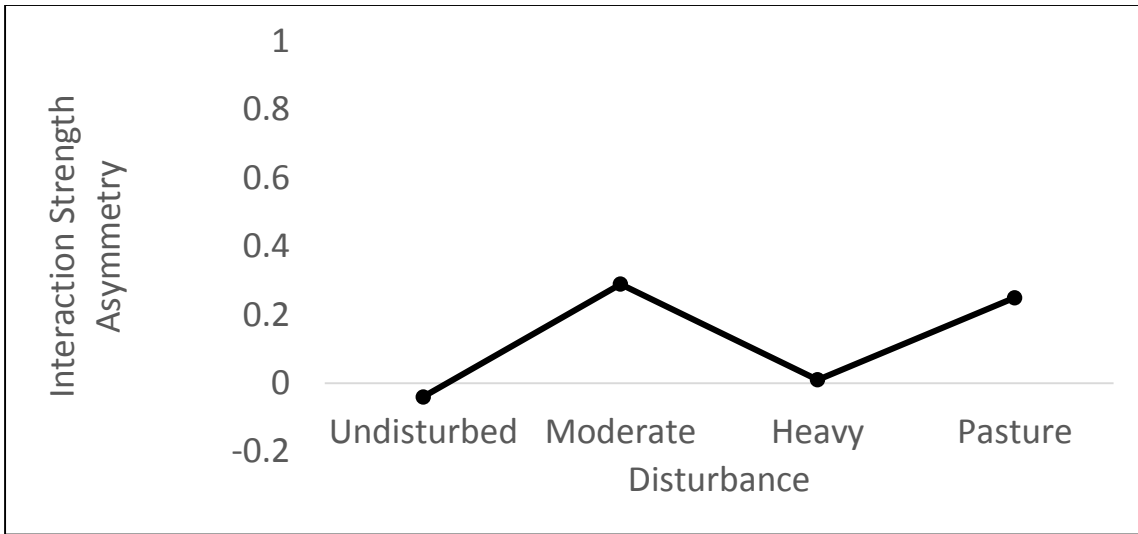
APPENDIX D: NETWORK ANALYSES WITH APIS MELLIFERA REMOVED



Appendix D 1. Network specialization scores for each disturbance category with *Apis mellifera* removed from networks.



Appendix D 2. Nestedness scores for each disturbance category with *Apis mellifera* removed from networks.



Appendix D 3. Dependence (interaction strength asymmetry) scores for each disturbance category with *Apis mellifera* removed from networks.

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