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Ant Diversity and Community Structure in Coastal Dunes and Wetlands

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ANT DIVERSITY AND COMMUNITY STRUCTURE IN COASTAL DUNES AND WETLANDS

A Dissertation

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Agricultural and Mechanical College
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TABLE OF CONTENTS

ABSTRACT

How do many species live in a certain place? How does species composition changes among habitats? And what mechanisms decide species distribution? These are fundamental questions in community ecology. I first investigated ant diversity in two coastal ecosystems (dunes and wetlands) in the northern Gulf of Mexico, and then used the distribution patterns to infer assembly processes that structure ant communities in coastal areas. Specifically, the following hypotheses are tested: (1) coastal systems support lower ant diversity due to the unsuitable environment; (2) species living near the seashore are a subset of those exist near inland; (3) deterministic processes are the dominant forces driving coastal ant communities.

Forty-six and 22 ant species were found in dunes and wetlands, respectively. Although some ants were associated with certain habitats, no species could be considered a coastal specialist. Clementsian was the best model describing how ants change along environmental gradient in dunes. This indicated that each habitat supported a unique ant assemblage. In wetlands, most ants living in marshes could also be found in swamps, which is consistent with the nested pattern.

Abiotic factors were the dominant forces that decide ant diversity and community structure. For example, wetlands are flooded most of the year, which eliminates the species nesting in the soil. In addition, the physical habitat structure of wetlands and dunes is simple because of the lower plant diversity. Niches are limited for ants to nest in and forage. Biotic factors, such as the influence of vegetation and species interactions, were weak because few mosaic patterns, pairwise co-occurrence, and correlation between ants and plants was detected in this study. The contribution of stochastic processes increased under the relatively benign environment (under bushes).

In addition, this research suggested that ants can be used as biological indicators in coastal dunes and wetlands. Fragmentation, habitat restoration, oil pollution, and invasive species all influenced ant diversity and community structure. Although the responses of ant assemblages to disturbances were situation-dependent, the common effect was the invasion of the red imported fire ant, *Solenopsis invicta* Buren, following disturbances.

CHAPTER 1. INTRODUCTION

1.1 Ant diversity in coastal ecosystems

Empirical ecological studies usually start with a description of the systems (Townsend et al. 2003). For example, the first step of biological diversity research is making an inventory of target organisms. Although we know well about the species distribution of some popular animals in many places (e.g., Green et al. 2013), major gaps still remain in the knowledge of the composition of many taxa (e.g., insects), not only in the remote places but also around populated areas such as the coast. Coasts are the land areas affected by a variety of marine conditions (Davis and FitzGerald 2004, Woodroffe 2002). This study focused on dunes and wetlands because these two ecosystems perform important ecological functions (e.g., supporting a wide variety of organisms, protecting inland areas) and have high economic values (Barbier et al. 2011, Gomez 2008). In addition, each system contains several habitats that occur in a relative small area, which provide an ideal system to test some ecological theories.

The first goal of this study is to explore the ant diversity and functional groups in dunes and wetlands in the northern Gulf of Mexico. Although coastal ecosystems have been studied intensively, most of the work focused on vegetation, sediment, hydrology, biogeochemistry, and economically important animals (e.g., Baldwin et al. 1996, Bianchi and Allison 2009, Goni et al. 1998, Platt et al. 2015, Shepherd and Myers 2005, Turner and Rabalais 2003). A species list is still unavailable even for the relatively well-studied insect groups such as ants (but see Colby and Prowell 2006, Hooper-Bùi and Pranschke 2006, Dash and Hooper-Bùi 2008). Ants have a worldwide distribution and high diversity (Hölldobler and Wilson 1990), and perform critical functions in ecosystems (Agosti et al. 2000, Lach et al. 2000). In addition, ant diversity strongly corresponds with that of other organisms (Majer 1983, Andersen et al. 1996, Schuldt and

Assmann 2010), and they are sensitive to habitat modification and respond to changes in ways similar to other taxa (King et al. 1998, Hoffmann et al. 2000, Andersen et al. 2004). All of these make ants useful bioindicators in environmental monitoring programs that aim to maintain or restore the ecosystem integrity. However, only a few studies focus on ant communities in coastal areas (Calcaterra et al. 2010, Cardoso 2010). As a result, chapters 2, 5, 6, and 7 started with describing ant diversity in each habitat.

1.2 Changes of ant assemblages along coastal environmental gradient

How and why diversity varies between locations is one of the core themes in community ecology (Mittelbach 2012). Although synthetic theories have been developed that try to explain the variations of species composition in nature (Chase and Myers 2011, Gravel et al. 2006, Vellend 2010), results from specific research can be inconsistent with the prediction of theories (e.g., Sara et al. 2006). More empirical studies are required to modify and advance ecological theories in the future. In this dissertation, I focus on testing two related hypotheses addressing how ant assemblages respond to environmental gradients in coastal areas.

Hypothesis 1: ants show a nested pattern along coastal environmental gradients. The nested pattern hypothesis states that species in lower diversity sites are a subset of those in higher diversity ones. Nestedness was originally proposed to describe the effects of isolation on assemblages (Darlington 1957). Later, studies showed that an unsuitable environment can cause non-random local extinction (e.g., Worthen et al. 1998). Distribution pattern would be nested if most species in the harsh areas can also be found in the benign habitats. I generated this hypothesis based on my observation at the beginning of this project, which showed all ant species living in salt marshes can also be collected in swamps and bottomland hardwood forests.

Hypothesis 2: deterministic processes dominate ant assemblages in coastal areas. Dune and wetlands are not suitable habitats for ants because of the high disturbances and/or environmental stress (e.g., frequent storm surge and sand burying in dunes, flooding in salt marsh). Niche-based processes can be important forces that drive species distribution under harsh condition (Chase 2007). In this dissertation, I examined how ant interspecific interactions and vegetation, which have been proven that can affect ant communities greatly in other ecosystems (Lach et al. 2010), affect ant assemblage in each habitat (dunes: chapter 2 and 3; marsh: chapter 5 and 6; swamp: chapter 7). *Under the relatively benign environment, I assumed that the relative contribution of stochastic processes would increase*.

Coastal areas support the highest human density in the world (McGranahan et al. 2007, Small and Nicholls 2003). Inevitably, the coast suffers many types of anthropogenic disturbances. Urbanization, fragmentation, diversions, construction of canals, and sea level rise makes the coastal areas in the northern Gulf of Mexico among the most rapidly vanishing ecosystems in the US (Chambers et al. 2005, Chen et al. 2015, Day et al. 2000, Gosselink et al. 1998, Turner 1997, Walker et al. 1987). The last part of this study is to test if ants can be used as indicators to evaluate how human disturbances, such as habitat reconstruction and isolation (chapter 4), oil pollution (chapter 4), and invasive species (chapter 6 and 7) affect coastal systems.

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CHAPTER 2. ANT DIVERSITY AND COMMUNITY STRUCTURE IN COASTAL DUNES OF THE NORTHERN GULF OF MEXICO[1]

2.1 Introduction

Coastal dunes have a worldwide distribution and protect areas further inland from erosion by waves and wind (David and Fitzgerald 2004). Dunes support high ecological diversity and contain many endemic and endangered species due to their geomorphological and environmental heterogeneity (Powell 1981, Lichter 1998, Van der Maarel 2003). However, they are fragile ecosystems and suffer from many kinds of natural and anthropogenic disturbances including hurricanes, invasive species, global sea-level rise, urbanization, and improper management (Feagin et al. 2005, Grunewald 2006, Banna and Mahmoud 2008, Bonte and Maes 2008, Claudino-Sales et al. 2008, Marchante et al. 2008, Jackson and Cooper 2011, Provoost et al. 2011).

Some distinguishing characteristics of these areas are the environmental and vegetation gradients that run perpendicular to the seashore and create discrete, parallel zones of habitation in a relatively small area (Hesp 1991,Dech and Maun 2005, Lane et al. 2008). Each zone has its own plant composition that is able to withstand the biotic and abiotic stressors in that given area (Wilson and Sykes 1999, Maun 2009, Miller et al. 2010). Generally, a few herbaceous pioneer plants dominate the foredunes, and backdunes yield a higher diversity with woody species becoming more abundant (Kerley et al. 1996, Maun and Perumal 1999, Isermann 2011, Mondino et al. 2011). The decreased physical stress and more complex vegetation structure in the backdunes create more available habitats. As a result, faunal diversity and complexity of food

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[1] This chapter previously appeared as Chen X, Adams B, Bergeron C, Sabo A, Hooper-Bui L (2015) Ant community structure and response to disturbances on coastal dunes of Gulf of Mexico. Journal of Insect Conservation 19 (1):1-13.

webs increase with distance from the ocean (Gaylard et al. 1995, Slawska 1997, Yoshitake and Nakatsubo 2008, Rajaniemi and Allison 2009). Coastal dunes have often been used in primary succession studies to examine changes of diversity and community composition, and species replacement (Duffy 1968, Boomsma and Van Loon 1982, Johnson 1997). However, the rates of succession and responses to the various gradients are not the same for different groups of organisms (Slawska 1997, Bonte et al. 2004, Isermann 2005, Lane et al. 2008). Compared to the well-studied soils and plant succession, much less is known about invertebrate changes not only in coastal dunes, but also in other primary succession sites (Kaufmann 2001).

Ants (Hymenopera: Formicidae) are among the most numerically abundant creatures in nature, but have received much less attention than plants, spiders, birds, mammals, and soil microorganisms on coastal dunes. However, ants play important ecological functions in these ecosystems. For example, they act as soil engineers by affecting soil lime content, thickness of the organic layer, and compactness (Bonte et al. 2003); they compete for food with crabs and other arthropods (Morrison 2002), disturb turtle nests (Wetterer et al. 2007); decrease the herbivore population (Oliveira et al. 1999, Lehouck et al. 2004); transport seeds, and influence plant germination, reproductive success, and distribution patterns (Oostermeijer 1989, Bonte et al. 2003, Cuautle et al. 2005). They also engage in many mutualistic associations with other creatures (Crutsinger and Sanders 2005, Rico-Gray et al. 2007). Therefore, given that few studies have investigated ants on coastal dunes — none along the northern Gulf of Mexico — the goal of this research was to characterize ant diversity, community structure, and how environmental factors, especially vegetation structure, influence ants on dunes.

2.2 Methods

2.2.1 Study sites and sampling methods

Three sampling sites along the north Florida coast were selected: Saint Joseph Peninsula Preserve State Park, Saint Andrews State Park, and Grayton Beach State Park. Those coastal dune systems consist of distinct plant communities that were divided into four habitats: foredunes, slacks, open ground of backdunes, and bush areas of backdunes (Figure 2.1). The first three habitats are open areas dominated by herbaceous species such as *Ipomoea stolonifera* J.F.Gmel, *Panicum amarum* Elliott, *Uniola paniculata* L., and *Paspalum vaginatum* Sw. Bush areas of the backdunes are shady due to the occurrence of *Quercus geminata* Small.

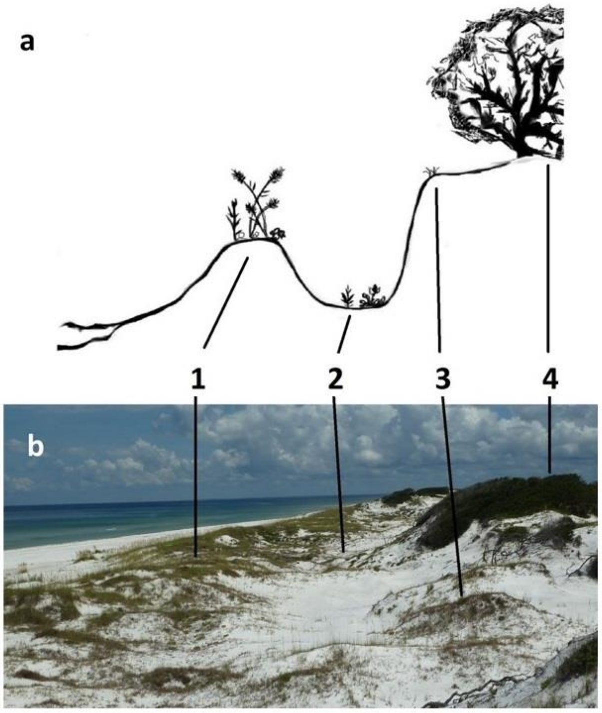

Figure 2.1 **a)** Schematic representation of coastal dunes. **b)** Coastal dunes in Saint Joseph Peninsula Preserve State Park, Florida. **1** Foredune, **2** Slack, **3** Backdune (open ground), and **4** Backdune (bush).

Quadrat sampling and hand collecting were the primary methods used in this study because of the large variation of vegetation structure of each habitat. Pitfall traps and baiting, the most common collection methods in invertebrate studies, could not be used because setting baits and digging are forbidden on coastal dunes in addition to the problem of disturbance due to tides and shifting sands. Winkler, another common method, was not suitable because no leaf litter occurs in foredunes and slacks.

Transects along the foredune, slack, and open ground of the backdunes were created. Each transect, which was parallel to the shoreline, was composed of seven to ten plots (0.6m x 0.6m quadrats) separated by at least 10m. Variations in the total number of plots per transect were because of time limitations (explained below). If an ant nest or foraging trail was found within 1.5m of a plot location, then that plot was not used. All ants on the ground or on the plants within the quadrat were collected by aspirator and stored in 95% ethanol, which would take about one minute. Environmental factors that may influence ant presence were also measured. These included the time of day, temperature, relative humidity, and plant structure (species, stem number, maximum and average height, and presence of flowers). A photograph from 1m above the quadrat was also taken to determine the percent vegetation coverage in each plot. All sampling occurred between 8:00am and 12:00pm to standardize collection and reduce variation due to time or temperature differences. Opportunistic hand collecting was conducted for one hour in each habitat after all quadrat sampling was complete.

Plots in the bush areas were selected based on the presence of leaf litter and canopy cover, as well as isolation from surrounding bushes (eight plots in Saint Joseph Peninsula Preserve State Park, six in Saint Andrews State Park, and five in Grayton Beach State Park). A quadrat sample (0.6m x 0.6m) was taken at each plot. Temperature, relative humidity, and leaf litter depth (at each corner and the middle of the quadrat) were recorded. All leaf litter within the quadrat was then transferred to a plastic container to prevent ants from escaping. An initial inspection for ants was conducted on the leaf litter. Any ants seen in the leaf litter were immediately collected. The leaf litter was then sifted in small batches through a mesh screen (0.5cm x 0.5cm) into a different plastic container. All ants from the sifted leaf litter were collected and stored in 95% ethanol. The quadrat sampling under the bush would take about 1.5 to 2 hours per plot. The leaf litter was then stored in a plastic bag and taken back to the lab for further analysis including measuring dry weight and determining the number of species of plants represented by the leaves in the sample. Information about vegetation structure (distance from center of quadrat to the three nearest bushes, the circumference of bush trunks, and the height of the lowest live branch) was then documented. Opportunistic hand-collecting and beating on and around bushes were also performed on the backdune.

2.2.2 Data analysis

Rarefaction and extrapolation curves were generated to compare ant species richness among foredune, slack, open ground of the backdune, and area under the bushes in the backdune using EstimateS (Colwell 2013, the number of samples was extrapolated in each habitat to 42 based on Chao 2). Data from quadrat sampling and hand collecting were pooled to maximize species richness (Gotelli and Ellison 2012). Richness was also compared among the four habitats using analysis of variance (ANOVA) in SAS 9.3 (PROC GLIMMIX). To assess sampling completeness, incidence-based coverage estimator (ICE) and Chao2 were calculated for each habitat using EstimateS. Rényi diversity profiles were performed using Biodiversity R (Kindt and Coe 2005, R Core Team 2013) to study the differences of diversity among habitats. The Rényi profile is a useful method for diversity ordering, and can provide more information than single a diversity index (Tóthmérész 1995, Ricotta 2003, Kindt et al. 2006). In the profile, each line represents the diversity of one habitat, the higher position of the line represents the higher diversity of that habitat. It is not possible, however, to order the diversity when the lines intersect. Ant species were assigned to functional groups as described by Andersen (1997) and Hoffmann and Andersen (2003).

Patterns of species composition of ant assemblages were investigated using multivariate analysis with Program PAST (Hammer et al. 2001). Two-dimensional ordination with Detrended Correspondence Analysis (DCA) and non-metric multidimensional scaling (NMDS) were conducted to assess the species composition among habitat plots, followed by Analysis of Similarities (ANOSIM) to detect the differences of composition among sites. Only presence/absence data was used to do the above analysis (Gotelli et al. 2011).

Ant richness, relative abundance (individuals per quadrat), and vegetation structure (open area: plant richness, stem number, plant cover, maximum and average stem height, and flowering or not; bush area: litter depth, litter dry weight, distance between quadrat to closest bush, trunk circumference of that bush, and canopy height) were analyzed using multiple linear regression in SAS (PROC REG). Both backward and forward selections were used to determine the most closely related vegetation variables. Ant species richness and relative abundance, plant richness and stem number were log-transformed before analysis to ensure normal distribution.

2.3 Results

2.3.1 Species diversity, community structure, and functional groups

A total of 3854 individuals representing 44 species, 24 genera, and 6 subfamilies were collected (Table 2.1). The richest subfamily was Myrmicinae, which included 23 species from 12 genera. Species richness per habitat was 6, 6, 9, and 39 in foredunes, slacks, open ground of backdunes, and backdunes under bushes, respectively. Rarefaction and extrapolation curves approached an asymptote for open areas (foredunes, slacks, and open ground of backduness), but not for bush areas (Figure 2.2, see Appendix A for confidence intervals and standard deviation). The ICE and Chao2 also estimated that the majority of ants in the open areas were collected. However, six to nine species may have been missed in/under bushes (Table 2.2). The species richness under bushes was significantly higher than that in other habitats (ANOVA, $F_{3,70}$=13.30, df=3, $P<0.0001$), but was similar among open areas. In addition, the Rényi profile indicated bush areas supported the highest diversity, followed by the open ground of backdunes (Figure 2.3). The most numerous species in open areas were *Dorymyrmex flavus* McCook and *Forelius pruinosus* (Roger). *Pheidole dentata* (Mayr) was the most common ant under the bushes of the backdunes, followed by *Trachymyrmex septentrionalis* (McCook) and *Aphaenogaster ashmeadi* (Emery). The least abundant species across all research sites were *Aphaenogaster floridana* Smith, *Stigmatomma pallipes* (Haldeman), and *Temnothorax texanus* (Wheeler), each represented by fewer than five individuals.

Table 2.1 Functional groups with assigned ant species. For each species, information is provided on its habitat(s): FD foredunes, SL Slack, BO Backdune (open ground), BB Backdune (bush).

Functional Group	Species	FD	SL	BO	BB
Dominant Dolichoderinae	*Forelius pruinosus*	X	X	X	X
Subordinate Camponotini	*Camponotus impressus*				X
	Camponotus socius				X
	Camponotus floridanus	X			X
Generalized Myrmicinae	*Crematogaster ashmeadi*				X
	Crematogaster pilosa				X
	Crematogaster pinicola				X
	Monomorium minimum	X		X	X
	Pheidole dentata			X	X
	Pheidole floridana				X
	Pheidole morrisii				X
Hot Climate Specialists	*Pogonomyrmex badius*		X	X	
Cold Climate Specialists	*Temnothorax texanus*		X		
	Temnothorax pergandei				X
Tropical Climate Specialists	*Cyphomyrmex rimosus*				X
	Trachymyrmex septentrionalis			X	X
	Pseudomyrmex ejectus				X

(Table 2.1 continued)

Functional Group	Species	FD	SL	BO	BB
	Pseudomyrmex gracilis				X
	Pseudomyrmex pallidus				X
Cryptic Species	*Stigmatomma pallipes*				X
	Brachymyrmex depilis				X
	Brachymyrmex patagonicus				X
	Pheidole moerens				X
	Pyramica dietrichi				X
	Strumigenys talpa				X
	Solenopsis carolinensis			X	X
	Strumigenys louisianae				X
	Hypoponera opacior				X
Opportunists	*Dorymyrmex bureni*	X	X	X	X
	Dorymyrmex flavus	X	X	X	
	Tapinoma melanocephalum				X
	Formica pallidefulva				X
	Formica archboldi				X
	Nylanderia arenivaga	X	X	X	X
	Nylanderia sp.				X
	Nylanderia parvula				X
	Nylanderia phantasma				X
	Nylanderia wojciki				X
	Aphaenogaster ashmeadi				X
	Aphaenogaster floridana				X
	Odontomachus brunneus				X
	Odontomachus haematodus				X

Table 2.2 Species richness estimators with their standard deviations (SD) of four habitats of coastal dunes, Sobs Total number of species observed in the habitat, ICE Incidence-based Coverage Estimator.

Habitats	Sobs	ICE	ICE (SD)	Chao 2	Chao 2 (SD)
Foredune	6	6.83	0.01	6	0.16
Slack	6	7.8	0.01	6.96	2.14
Backdune (open ground)	9	10.87	0.01	10	1.87
Backdune (bush)	39	47.77	0.01	44.79	5.04

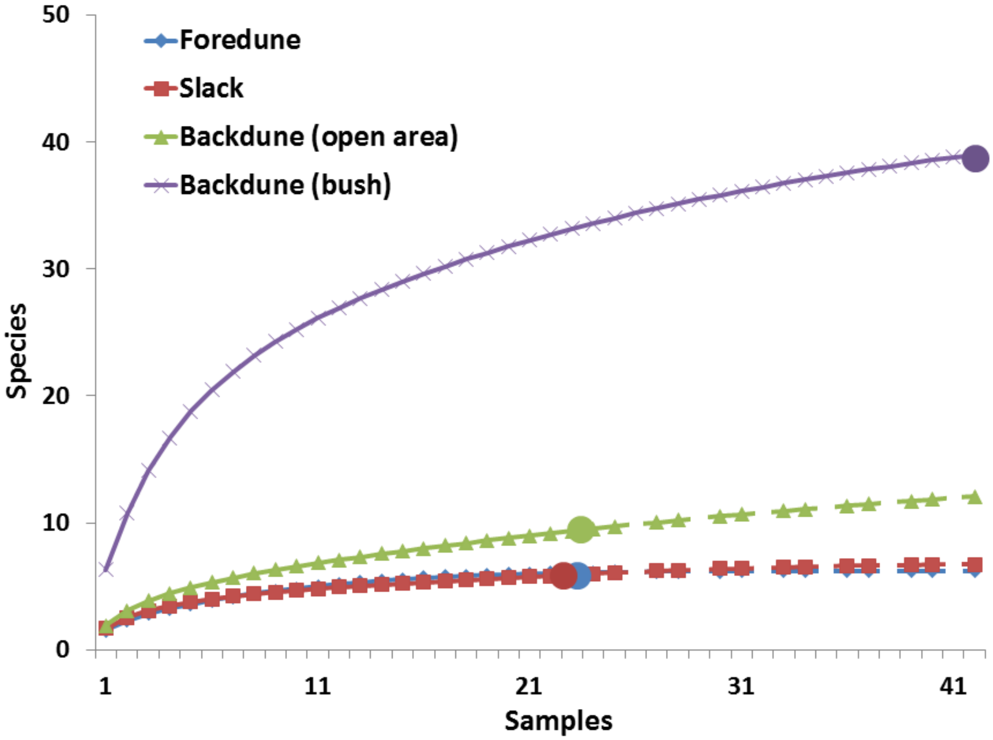

Figure 2.2 Sample based rarefaction (solid lines) and extrapolation (dashed lines) curves for reference samples (filled circles) of the four habitats that are based on an average of 1,000 randomizations of the data. See Appendix A for details.

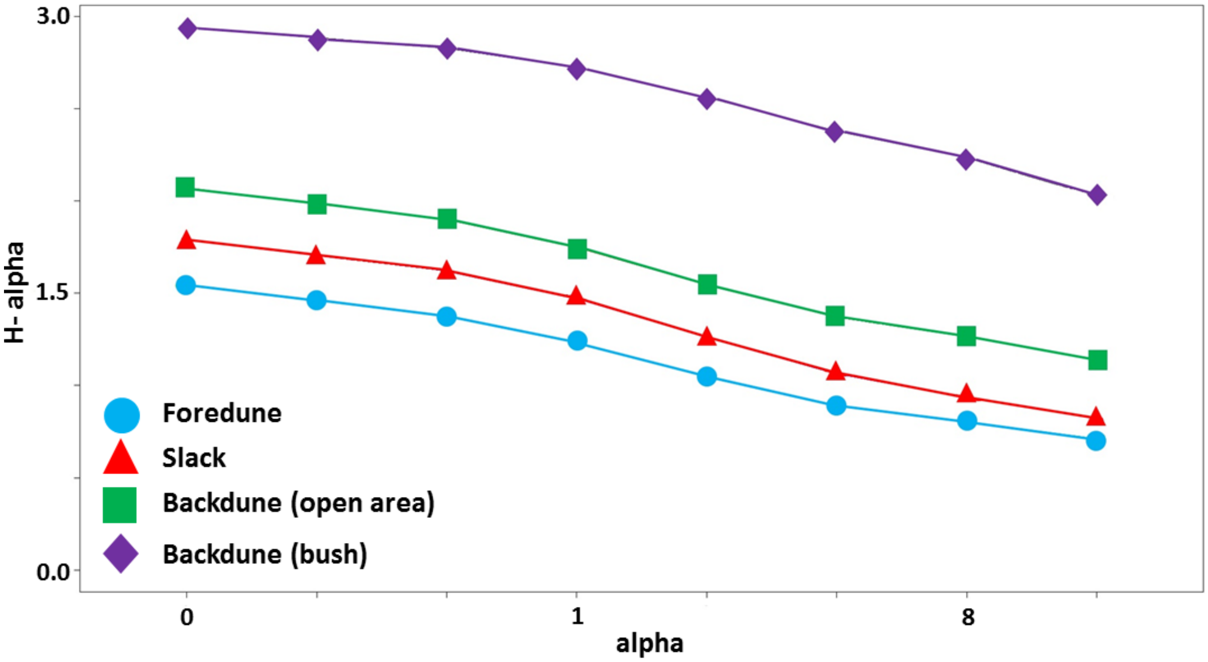

Figure 2.3 Rényi diversity profiles for the different habitats of coastal dunes along Gulf of Mexico.

DCA and NMDS produced similar results, and only the DCA analysis is shown here. The graph showed two distinct ant communities (Figure 2.4). Plots of foredunes, slacks and open ground of backdunes overlapped (but the dots of open ground of backdunes were closer to those of bush). Plots of bush area separated from those of open areas. One-way ANOSIM further confirmed that the species composition of bush areas is significantly different from other habitats (Jaccard Index, R=0.2882, P<0.0001).

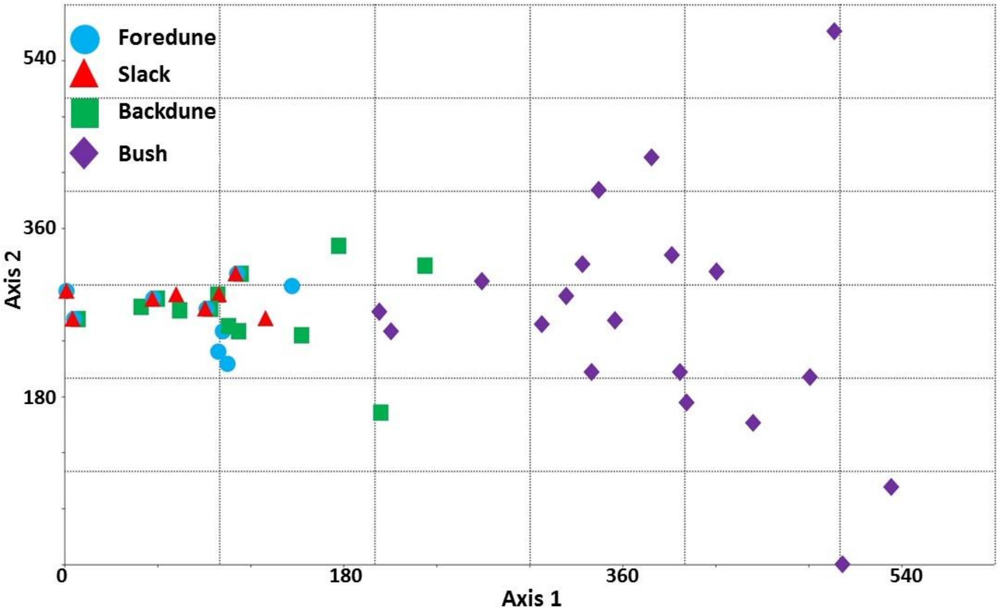

Figure 2.4 Detrended Correspondence Analysis (DCA) for ant species composition based on quadrat sampling in four dune habitats, only presence/absence data was used, each dot represented the species composition in each plot.

Eight of Andersen's functional groups were found in the research sites (Table 2.1). These included Dominant Dolichoderinae (one species), Subordinate Camponotini (3), Generalized Myrmicinae (7), Tropical Climate Specialists (5), Hot Climate Specialists (1), Cold Climate Specialists (2), Opportunists (14), and Cryptic Species (10). *Solenopsis invicta* Buren was placed in a new functional group: Dominant Invasives, and placed *Pheidole moerens* (Wheeler) in Cryptic Species based on their biological characters such as body size, limited interactions with other ants, and personal communication with Dr. Allen Andersen. Dominant Dolichoderinae and

Opportunists were the only two groups that appeared in all habitats, and Opportunists were the most frequently sampled. Cryptic Species and Tropical Climate Specialists only occurred in backdunes. Bush areas supported more groups than other habitats (Figure 2.5).

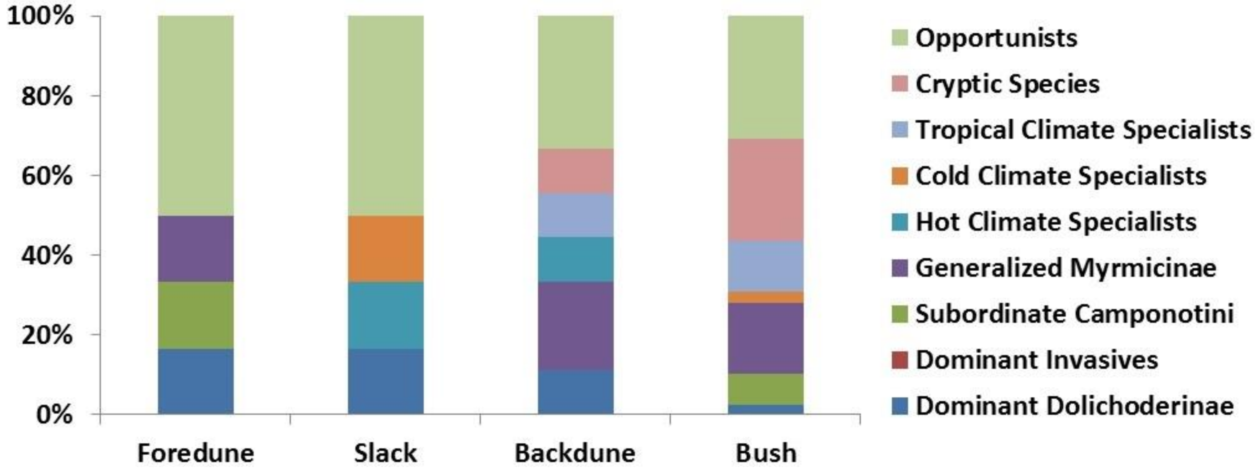

Figure 2.5 Functional group profiles of coastal dune ant fauna from four habitats. Data are relative contributions of each functional group to total species richness.

2.3.2 Ant and vegetation relationships

No significant correlation was detected between ant diversity and plant structure in foredunes. In slacks, ant relative abundance was significantly correlated with plant richness (P=0.0093, sr^2 Type II =0.212). In the open ground of backdunes, ant relative abundance was significantly correlated with plant cover (P=0.0156, sr^2 Type II =0.012), plant richness (P=0.0009, sr^2 Type II =0.027) and stem maximum height (P=0.0165, sr^2 Type II =0.012); ant richness was significantly correlated with plant richness (P=0.0072, sr^2 Type II =0.156). In the bush areas, ant relative abundance was significantly correlated with nearest trunk circumference (P=0.0176, sr^2 Type II =0.177); ant richness was significantly correlated with nearest trunk circumference (P=0.0080, sr^2 Type II =0.183) and lowest canopy height (P=0.0286, sr^2 Type II =0.114).

2.4 Discussion

Ant species diversity increases moving inland from the water's edge. The bush areas in the backdunes support the highest diversity and unique species assemblages. This is best explained by the presence of leaf litter and canopy acting as keystone structures (Tews et al. 2004). These structures may provide the increased niche availability, a more stable environment, and increased moisture retention that strongly influence the distributions of many other organisms (Pollet and Grootaert 1996, Sarig et al. 1999, Finke and Snyder 2008, Carpintero et al. 2011, Schirmel and Buchholz 2011).

All known functional groups of ants can be found in the coastal dunes with the exception of Specialist Predators. The Opportunists was the most diverse functional group across all of the different habitats. This is because of the ability of Opportunist ants to withstand consistent, natural disturbance (such as sand burial and strong winds) on coastal dunes. Subordinate Camponotini, Tropical Climate Specialists, most Generalist Myrmicinae, and most Cryptic Species were found only in the bush areas of backdunes due to the complexity of the vegetation structure and the available nesting sites provided by the canopy and leaf litter. The disappearance of the Hot Climate Specialists from the bush areas is expected because they are associated with open, hot, and stressed habitats (Pfeiffer et al. 2003, Gomez and Abril 2011). One unexpected finding was a cold climate specialist species (*T. texanus*) located in the slack at Grayton Beach State Park. These ants are normally associated with mesic or shady environments (So and Chu 2010, Beaumont et al. 2012). Grayton Beach State Park has a narrow slack area very close to the backdunes. Because of this, *T. texanus* may nest in the bush areas immediately next to the slack. Further collections need to be made to confirm this.

Vegetation is one of the most important factors influencing ant distribution at local, regional, and continental scales (Gotelli and Ellison 2002). Vegetation structure alters food resources, nesting sites, and micro-climate conditions (Boomsma and Devries 1980, Rico-Gray and Garcia-Franco 1998, Andersen et al. 2006, Hoffmann and James 2011), and further regulates ant diversity, behavior, and interactions among species (Huxley and Cutler 1991, Botes et al. 2006, Wilkinson and Feener 2007, Hill et al. 2008). The general assumption is that species diversity is positively associated with vegetation complexity (Bonte et al. 2002, Tews et al. 2004, Sarty et al. 2006). However, the local environment, habitat type, plant composition, disturbance, as well as ant behavior and life history make the outcomes highly variable (Bestelmeyer and Schooley 1999, Kotze and Samways 1999, Retana and Cerda´ 2000, French and Major 2001, Lassau and Hochuli 2004). In addition, most previous research has been conducted in environments strongly associated with anthropogenic disturbances such as fire and grazing, and less attention has been paid to more natural habitats (Ruiz-Jaen and Aide 2005, Jiménes-Valverde and Lobo 2007, Gibb and Parr 2010).

In coastal dunes, vegetation structure significantly influenced the ant community. On open areas, increased stem height, plant richness and cover are related to higher ant diversity. This may be due to increased niche opportunities or improved micro-climates caused by the larger three-dimensional structure associated with the various kinds of vegetation (Lawton 1983, Gardner et al. 1995, Vasconcelos et al. 2008, Wenninger and Inouy 2008, Cardoso et al. 2010, Wiezik et al. 2011). More importantly, it also may be an indicator of an area experiencing less stress. Vegetation may also influence ants indirectly. Higher diversity of plants may attract other arthropods, which function as food resources, competitors, or predators of ants (Hansen 2000). In addition, this research only covered a range of plant cover from zero to 58 percent, and plant richness from zero to six in a single plot. Further studies are needed to determine if the relationship between ant diversity and plants is maintained at more complex vegetation structure (Lassau and Hochuli. 2004, Arnan et al. 2007, Hill et al. 2008). Although ant community composition is similar among the open area of dunes, the relationship between ant diversity and vegetation structure is not consistent in these habitats. Higher correlations are found in the later succession stages, this may be due to the decreasing environmental stress from foredune to backdune. However, manipulative experimental approaches are needed to confirm this assumption and to reveal other possible explanations (Luque and Lopez 2007).

Ant diversity increases sharply when bushes inhabit the backdunes. Whereas no associations were detected between ant diversity and leaf litter, which is thought to play an important role in structuring ant composition (Bestelmeyer and Schooley 1999, Cardoso et al. 2010), ant richness was higher under thicker bushes. The thicker trunk may reflect the age of bushes as well as the age of sampling site as older bushes will have a larger trunk circumference. The sites with longer succession time may be more stable and support more species (Maun 2009).

General ecological and conservation theories together with detailed descriptions of local environments, habitats and vegetation types, and the reaction of local species to habitat changes should be considered when making protection policies (Dauber et al. 2006). This research indicates that plant structure significantly influences ant composition on coastal dunes. In the northern Gulf of Mexico, invasive species, dune restoration activities, and oil pollution modify or simplify the plant composition in dunes (Cousins et al. 2010, Grafals-Soto 2012, Hooper-Bùi, unpubl.). In addition, the frequency and strength of hurricanes and storm surge events have increased and will continue increasing in the future because of global climate change (Trenherth

2005, Webster et al. 2005). Hurricanes and storm surge are predicted to change the vegetation across the whole dune system (Gornish and Miller 2010). The changed vegetation structure may affect ant diversity, and further influence the dune ecosystem due to the important ecological roles that the ants play.

Ant diversity increases with accumulating complexity and richness of vegetation and reduction of stressors. In the bush areas of the backdunes, increased ant species diversity results mainly from the existence of the canopy and leaf litter, which provide complexity and buffer from stress. These structures provide increased niche space and play crucial roles in supporting high diversity of not only ants, but also other fauna (Hansen 2000, Ruiz-Jaen and Aide 2005, Silva et al. 2011). This study emphasizes the importance of protecting backdunes, which act as critical habitats but are frequently disturbed in northern Gulf of Mexico (Pries et al. 2009). Additionally, backdunes are important for wind attenuation and to protect inland areas from storm surge.

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CHAPTER 3. CHANGES OF ANT COMPOSITION AND ASSEMBLY PROCESSES IN COASTAL DUNE

3.1 Introduction

One active study field in ecology and conservation biology is to investigate how species composition and functional groups change along disturbance and/or stress gradients (Walker and del Moral 2003). It will get more attention in the future given the increasing anthropogenic disturbances globally (Keppel et al. 2012, Paillet et al. 2010, Prach and Walker 2011, Wilson et al. 2006). Although ecologists uncovered some general trends (e.g., intermediate disturbance hypothesis, stress-gradient hypothesis), results from different studies have, to some extent, been inconsistent (e.g., Fox 2013ab, Sheil and Burslem 2013). And the outcome may vary depending on the disturbance regimes, study organisms, the range of gradient, and scale (Brown and Jumpponen 2014, Chase and Myers 2011, Lepori and Malmqvist 2009).

Chapter 2 elucidated ant diversity and community structure in coastal dunes. Here, I focus on how ant distribution changes responding to the dune environmental gradient. Although several methods have been developed to study the distribution patterns, most of them only assess if one idealized model, such as a checkerboard or nested model, best fits the observed patterns (e.g., Diamond 1975, Ulrich et al. 2009). The pattern-based approach of metacommunity study (elements of metacommunity structure, EMS) can evaluate multiple competing models at the same time, and find the best one that summarize the species distribution along environmental gradients or among multiple habitats (Henriques-Silva et al. 2013, Leibold and Mikkelson 2002). So far, six idealized models (checkerboard, random, nested, evenly spaced, Gleasonian, and Clementsian) have been identified based on the degree of (1) species absence along gradient (coherence); (2) species replacements between sites (turnover); and (3) the boundaries of species group’s range (clumping) (see Leibold and Mikkelson 2002 and Presley et al. 2010 for details).

The first mission of this chapter is to identify which one best fits the change of ant composition from foredune to bush.

Revealing the underlying mechanisms that drive species distributions is an essential goal in community ecology (Mittelbach 2012). Environmental conditions and biotic interactions (deterministic or niche-based processes) have long been considered to largely determine species diversity and composition (Chase and Leibold 2003). Within the last half century, more attention has been paid to dispersal and drift (stochastic or neutral processes) as additional important explanations of community assembly, because of the development of Island Biogeography Theory, succession models, Neutral Theory, and metapopulation and metacommunity concepts (Leibold et al. 2004, Hubbell 2001, Mittelbach 2012, Walker and Moral, 2003). A growing body of literature has shown that neither niche nor neutral theory alone can fully explain species distributions in nature (Adler et al. 2007, Ellwood et al. 2009, Ingimarsdottir et al. 2012, Lord et al. 2000, Marquez and Kolasa 2013, Stokes and Archer 2010). Deterministic and stochastic processes more likely represent the opposite ends of a continuum (Gravel et al. 2006), and communities can be found at certain points along this spectrum based on the varying contributions of each process (e.g., Chase 2014, Freestone and Inouye 2015, Larsen and Ormerod 2014, Lindo and Winchester 2009, Mori et al. 2013, Morris 2005, Ruhí et al. 2012, Stegen et al. 2010,). Although many studies tried to uncover which process dominant in certain habitats, it is still poorly understood how the assembly processes change along environmental gradient (Vanschoenwinkel et al. 2010). The second goal of this chapter, therefore, is to uncover the mechanisms that drive ant distribution in dunes.

I tested these following hypotheses in this chapter: H_1: ant species in severer environment are a subset of that in more benign habitats. H_2: deterministic processes decide ant community near seashore, and the relative contribution of stochastic processes increases in the bush areas.

3.2 Methods

3.2.1 Study location and sampling methods

Five sampling locations along northern Gulf of Mexico were selected: Saint Joseph Peninsula Preserve State Park, Saint Andrews State Park, Grayton Beach State Park, Topsail Hill Preserve State Park, and Bon Secour National Wildlife Refuge (Figure 3.1). Those locations support intact dunes which contain foredune, slack, backdune, bush area, and maritime forest. Only the first four habitats were sampled in this study, because fire management was conducted in the maritime forests in the last ten years (personal communication with park rangers).

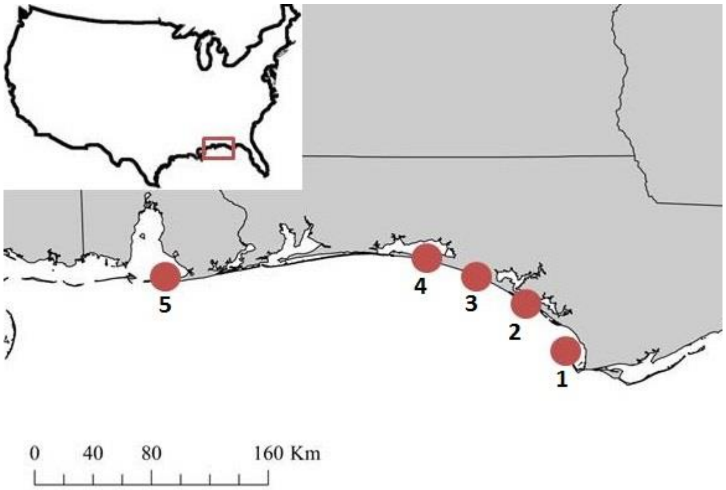

Figure 3.1 Study locations along northern Gulf of Mexico (red square in the contiguous US map shows the range of study sites). 1 Saint Joseph Peninsula Preserve State Park, 2 Saint Andrews State Park, 3 Grayton Beach State Park, 4 Topsail Hill Preserve State Park, and 5 Bon Secour National Wildlife Refuge.

The sampling methods were the same as described in Chen et al. (2015). In brief, transects were composed of seven to eight plots (0.6 m × 0.6 m quadrats, separated by at least 10 m) were created along the foredune, slack, and backdune. Ants in the quadrats were collected by using aspirators. Vegetation information— including plant cover, stem number, maximum and average height, and presence of flowers— of each species was recorded after ant sampling. One quadrat was set under each bush (six to eight in each location). Leaf litter within the quadrat was sifted (0.5 cm × 0.5 cm mesh screen) into a white plastic container. Ants found during the sifting and from the sifted litter were collected. Plant information— depth of leaf litter, distance from center of quadrat to the three nearest bushes, the circumference of bush trunks, and the height of the lowest live branch— were recorded after ant collecting. Hand collecting was performed after quadrat sampling in each habitat.

3.2.2 Data analysis

The results of Permutational ANOVA (PERMANOVA) and Non-metric multidimensional scaling (NMDS) showed that ant communities in Saint Joseph and Bon Secour were different from that in other three locations (Appendix B.1 to B.3). This may be because (1) hurricane Ivan hit Bon Secour in 2004 (Appendix B.4), and (2) storm surges and hurricanes affect Saint Joseph in a different way than other locations because it is in the peninsula. As a result, data from these two locations was eliminated from the following analysis.

The elements of metacommunity structure (EMS) was used to identify the ideal metacommunity structure (Leibold and Mikkelson 2002). The metacommunity structure was determined using coherence, range turnover, and range boundary clumping from a species incidence matrix which was ordinated via reciprocal averaging (Leibold and Mikkelson 2002, Presley et al. 2009). An α of 0.05 was used for all analyses. Analysis was performed using MatLab (code is available at http://faculty.tarleton.edu/higgins/documents/EMS.zip)

The β-diversity value can be used to infer how the assembly processes change along environmental gradients (Anderson et al 2011, Chase 2007, Chase and Myers 2011). Changes in “raw” β-diversity, however, can result from complex mechanisms such as changes in local (α) and regional (γ) diversity instead of altered underlying mechanisms (Chase 2010, Chase et al. 2011, Kraft et al. 2011). Therefore, in order to control for the difference of α-diversity among dune habitats, I used the modified Raup-Crick metric to quantify the ant community dissimilarity among sites. Briefly, species from the relevant pool were assigned to each site randomly, then the similarity was calculated based on presence/absence data and repeat several times to generate the null distribution. The comparison of the difference between real community and null expectation allows me to determine the degree to which observed β- diversity patterns deviate from stochastic assembly. Raup-Crick dissimilarity values (β_{RC}) close to zero may suggest that community assembly is highly stochastic, while larger absolute deviation (close to +1 or -1) likely means that deterministic processes play stronger roles (for details see Chase et al. 2011). The software R (version 3.2.3. http://www.R-project.org) was used to generate the dissimilarity indices. Analysis of variance (ANOVA) and Tukey’s HSD-test (PROC GLIMMIX) in SAS 9.3 was used to compare the β_{RC} among four habitats (Guo et al. 2014).

A pairwise based of species co-occurrence analysis was applied to examine ant species interaction in each habitat. The probabilistic model developed by Veech (2013) was used here. This approach generates the probability of the frequency that one species pair deviated from the observed co-occurrence frequency. This model has lower Type I and II error rates because it does not rely on certain data randomization (see more analysis detail in Veech (2013)).

3.3 Results

Metacommunity exhibited positive coherence and boundary clumping, and more turnover than the mean generated by the null model. This resulted in Clementsian structures (Table 3.1). The β_{RC} was closer to zero (least deviated from null model) in bush areas (average value: 0.1), and closer to -1 in foredunes (average value: -0.72). The β_{RC} in slack and backdune was similar to each other (average value is -0.37 and -0.29, respectively. $P = 0.31$), but significantly different from that in foredune and bush area ($P < 0.001$, Figure 3.2). Only one pair of non-random species co-occurrence was detected in all dune habitats (Table 3.2).

Table 3.1 Results of analyses of coherence, species turnover, and boundary clumping for ants from coastal sand dunes in three locations (Saint Andrews State Park, Grayton Beach State Park, Topsail Hill Preserve State Park) in the northern Gulf of Mexico. Significant results ($P < 0.05$) are bold. Sp: species, S: sites, Abs: number of absences, Rep: number of replacements, M: Morisita's index, SD: standard deviation.

Sp	S	Coherence				Turnover				Clumping	
		Abs	P	Mean	SD	Rep	P	Mean	SD	M	P
29	12	34	<0.001	97.6	19.2	1212	0.016	970	99	2.9	<0.001

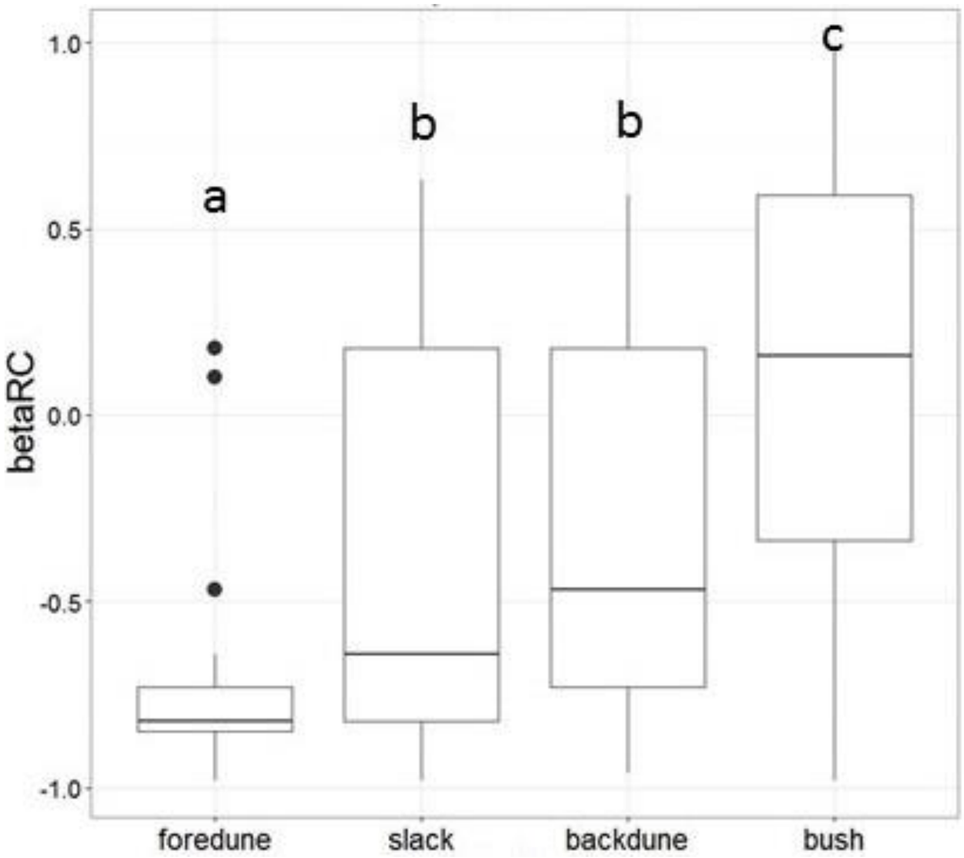

Figure 3.2 Raup-Crick dissimilarities (β_{RC}) of ant communities in difference coastal dune habitats. Different letters represent significant difference ($P < 0.05$).

Table 3.2 Results of a pairwise based analysis of ant species association in four coastal dune habitats along northern Gulf of Mexico.

habitat	number of species	quadrats	positive co-occurrence	negative co-occurrence	non-random (%)
foredune	7	20	0	0	0
slack	8	21	0	1	3.6
backdune	8	20	0	0	0
bush	25	19	0	0	0

3.4 Discussion

How species composition changes among habitats or along disturbance gradients is a "hot" topic in community ecology and biogeography (Lomolino et al. 2010, Mittelbach 2012). Disturbances can generate different species distribution patterns (Valanko et al. 2015, Ulrich et al. 2009). Nestedness was expected before I conducted this research because I assumed many ant species can colonize under bush where environment is begin. As harshness increases, sensitive ones would be filtered out and only disturbance tolerance species can survive in the foredune.

Contrary to my hypothesis, Clementsian is the best model that describes ant distribution along dune gradient, which indicates discrete communities exist in different habitats. At least two non-exclusive mechanisms can cause Clementsian pattern (Tonkin et al. 2015, Valanko et al. 2015). The first one is because species living in the same habitat have strong interdependent relationship, which seems unlikely here because the co-occurrence analysis showed that the species correlation was weak in all habitats. The second reason is that species have similar requirements for the environment, which I believe is true in this case because most ants found in the open ground (foredune, slack, and backdune) have the ability of nesting in the sand. Many species require leaf litter as nesting and/or foraging areas under the bush. For example, *Trachymyrmex* prefer to use oak catkins to cultivate fungi (Fisher and Cover, 2007). In addition, some arboreal ants (e.g., *Camponotus floridanus* (Buckley) and *Pseudomyrmex ejectus* (Smith)) were also collected in the litter, which increases the distinctness of species composition between open ground and bush areas.

Which type of assembly process (niche-based vs. random) is more important in a given habitat has received much attention recently not only in the field of basic ecological study but also conservation biology. Numerous studies suggested that deterministic processes dominate under harsh environment, and that stochastic events can be important in benign condition (e.g., Chase 2007). However, the opposite examples were also found in nature, and some studies indicated non-liner relationship between assembly processes and environmental gradient (Blaalid et al. 2012, Lepori and Malmqvist 2009, Wanner et al. 2008). In this study, I found that deterministic process is more important in the foredune. Given that the weak ant interspecific correlation (few pairwise co-occurrence) and little effect of plants on ant diversity (chapter 2), abiotic filters seems decide ant assemblages in the harsh areas. Sand burial, high solar radiation, and simple habitat structure can reduce the size of the realized colonizer pool, and only tolerant species that possess suitable traits or functions can persist, which leads to a more predictable community structure and lower variation of composition. For example, *Dorymyrmex flavus* and *Forelius pruinosus* (Roger) are the most common species in the foredune. They can forage on the exposed sandy ground which is too hot for other ants to walk on (chapter 2, www.antweb.org). These two species are omnivorous, and were observed carrying pieces of dead animal (small invertebrate or sea creatures) and collecting extrafloral nectar which seems the only food resources in foredune (Chen unpubl.).

The niched-based selective forces prevail until the occurrence of the bush which initiated a growing stochastic process in regulating ant assemblages. The leaf litter under the canopy increased the complexity of micro-environment, which can provide more shelters, food resources, and nesting sites for ants. More species in the regional pool have the potential to settle in this suitable habitat, and multiple species may have similar niche requirements. For instance, multiple species belonging to the same genus have similar body size and diet (e.g., *Strumigenys louisianae* Roger and *Strumigenys dietrichi* Smith, *Nylanderia parvula* (Mayr) and *Nylanderia phantasma* (Trager)). The occurrence of certain species, but not others in a specific site, more likely depends on the chance arrival of the initial colonizers and random local extinction events (Stokes and Archer 2010). The priority effect and drift cause greater variability in species composition, and increase the degree of randomness. In addition, higher stochasticity is expected when more rare species can be found in stable habitats (Lepori and Malmqvist 2009). In total, eight singletons were collected in this study and seven were found in leaf litter. The presence of those species could reduce the predictability between community composition and environmental factors, and reflects the stochasticity in the system (Silva et al. 2015, Chave 2004, Milner et al. 2011).

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CHAPTER 4. RESPONSES OF ANT COMMUNITIES TO DISTURBANCES IN COASTAL DUNES[2]

4.1 Introduction

Chapter 1 mentioned that, worldwide, coastal dunes are under multiple natural and anthropogenic disturbances (Figure 4.1). Urbanization and tourism in the northern Gulf of Mexico are two common human disturbances in dunes. Most of the backdunes and maritime forests have been destroyed due to road and building construction, and the remaining un-disturbed areas are small and located within parks (national or state). Foredunes can be found more often, but they are most commonly narrow strips reserved for recreational activities. Although re-building dunes is a hot topic in coastal restoration, most of the preservation strategies only focus on keeping or increasing the area; few are conducted to recover the ecosystem. The first part of this chapter will address how the loss of backdunes and dune planting affect ant communities in the dune. I assume the loss of back dune will not only decrease the diversity, but also change the ant community structure. The BP Deepwater Horizon oil spill occurred in 2010. Although many studies have documented the effects of oil on ecosystems (e.g., McCall and Pennings 2012), to my knowledge, no studies of oil on ants were conducted in dune habitats. On June 30, 2010, Hurricane Alex pushed oily seawater to the dunes in Grand Isle, Louisiana. Visible oil was left on the ground and vegetation after the water retreated. The second part of this chapter will uncover how oil pollution and beach cleaning activities influence ants in dunes.

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[1] Part of this chapter previously appeared as Chen X, Adams B, Bergeron C, Sabo A, Hooper-Bui L (2015) Ant community structure and response to disturbances on coastal dunes of Gulf of Mexico. Journal of Insect Conservation 19 (1):1-13.

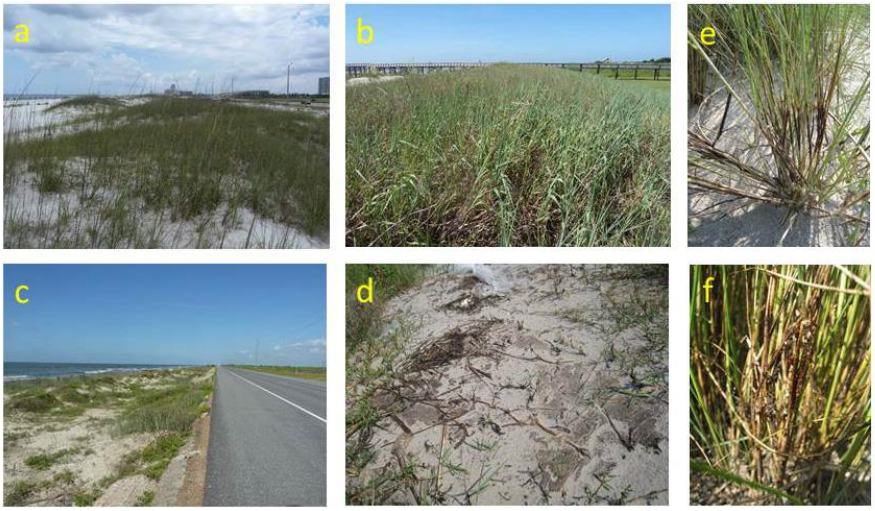


Figure 4.1 Dunes in **a** degraded (Gulf State Park), **b** planted (Grand Isle State Park), **c** re-built (Cameron Beach), and **d** oiled (Port Fourchon) areas. **e** and **f** showed the oil in plants (*Spartina Patens* (Aiton) Muhl) in Port Fourchon.

4.2 Methods

4.2.1 Study sites and sampling methods

The disturbed dunes were categorized as follows (Figure 4.2):

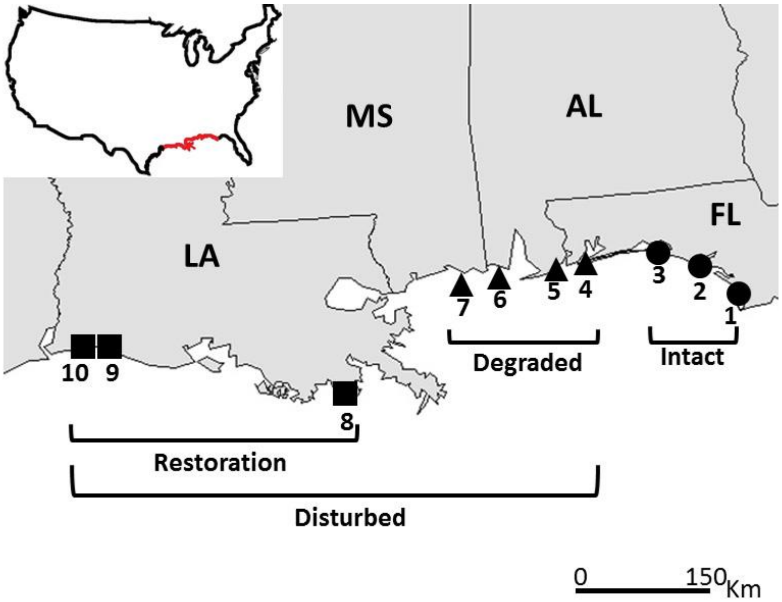


Figure 4.2 Location of study sites along northern Gulf of Mexico (red in the contiguous US map shows the range of study sites). 1 Saint Joseph Peninsula Preserve State Park, 2 Saint Andrews State Park, 3 Grayton Beach State Park, 4 Big Lagoon State Park, 5 Gulf State Park, 6 Dauphin Island, 7 Ship Island, 8 Grand Isle (young and old planted dunes), Grand Isle State Park and Port Fourchon (oiled dunes) 9 Cameron Beach (re-built dunes), and 10 Mae's Beach (young planted dunes).

(1) Degraded dunes: Big Lagoon State Park, Gulf State Park, Dauphin Island, and Ship Island no longer contain slacks and backdunes. These sites were labeled as degraded dunes. The foredunes on these sites were well protected, but are surrounded by areas of high human disturbance (tourist beaches, roads, and buildings). Intact dunes mentioned in Chapter 1 were used as the reference sites.

(2) Planted dunes: Dunes in Louisiana are poorly developed because the high frequency of disturbances caused by hurricanes and storm surges. *Panicum amarum* Elliott (bitter panicgrass) was planted in some areas of Grand Isle and Mae's Beach to restore the dunes, and labeled as planted dunes (areas planted less than three years before the time of study were called young-planted sites— found in both Grand Isle and Mae's Beach, sites more than six years old were termed old-planted sites— present only in Grand Isle).

(3) Re-built dunes: Most of Cameron Beach (very close to Mae's Beach) was re-built three years ago before the study (2010), and labeled as re-built dunes.

Planted and re-built areas were also called restoration dunes. In restoration areas, the dunes located in State Parks or wildlife refuges were used as the references and used to evaluate how restoration actions affect ants (Landi et al. 2012).

(4) Oiled dunes: Dunes in Grand Isle State Park and Port Fourchon were polluted by oil after Hurricane Alex, and labeled as oiled dunes.

I used the same methods described in Chapter 1: transects that parallel to the shoreline were created along the disturbed dunes. Each transect was composed of seven to ten plots (0.6m x 0.6m quadrats) separated by at least 10m. All ants on the ground or on the plants within the quadrat were collected by aspirator and identified to species in lab. All sampling occurred between 8:00am and 12:00pm to standardize collection and reduce variation because of time or temperature differences. Ants in degraded, planted and re-built dunes were collected in 2012 and 2013. In oiled areas they were collected before and shortly after (2010), and long after (2013) oil pollution occurred.

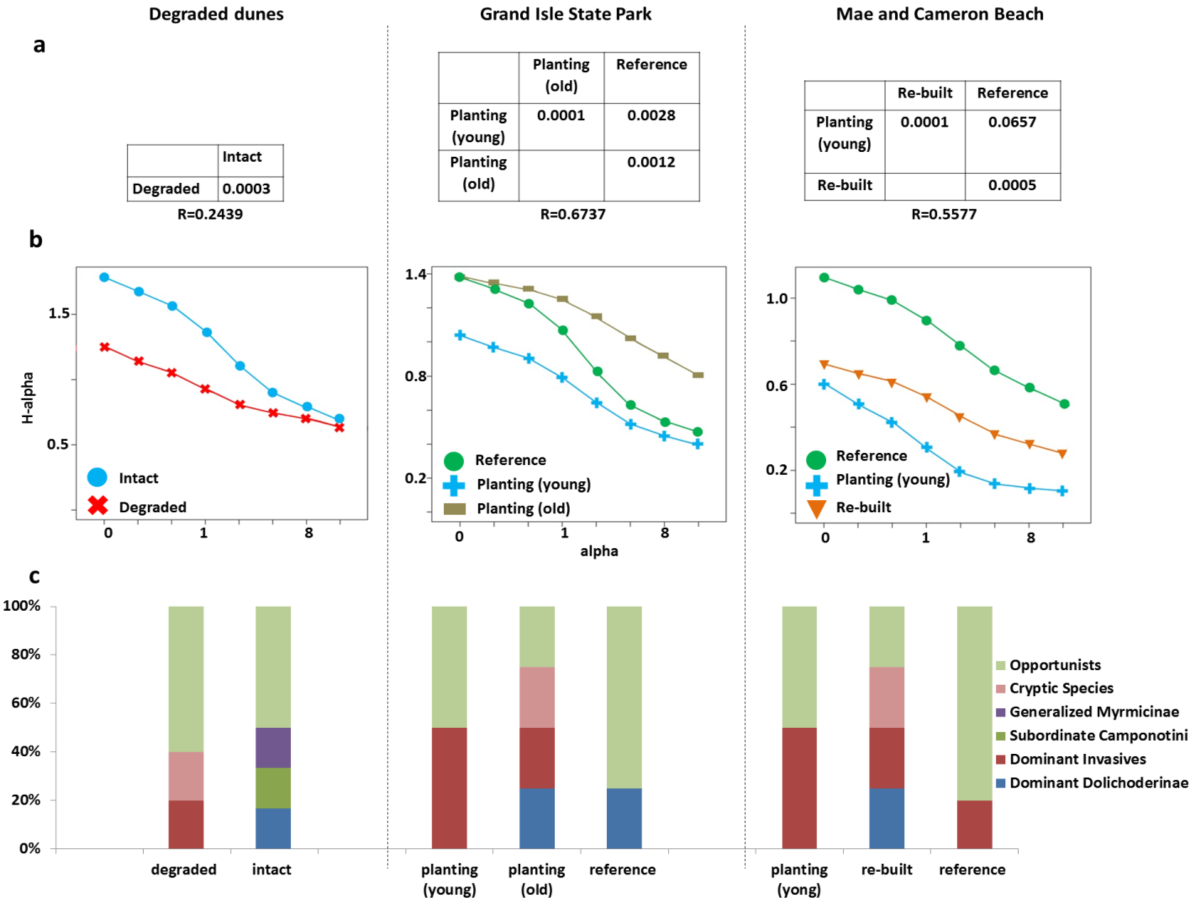
4.2.2 Data analysis

Rényi diversity profiles, functional groups, and Analysis of Similarities (ANOSIM) were used to study how ants responded to dune degradation, planting, and dune re-building (intact vs. degraded dunes, and reference vs. restoration sites). Rényi diversity profiles, functional groups, non-metric multidimensional scaling (NMDS), and one-way Permutational Multivariate Analysis of Variance (PERMANOVA) were used to determine the effects of oil pollution on ant communities. The analysis was conducted using R (R Core Team 2013, Package BiodiversityR) and PAST (Hammer et al. 2001).

4.3 Results

Ant diversity was lower in the degraded and restoration sites, but not in, old planted dunes (See b. in Figure 4.3). Community composition was different between intact and degraded dunes, and between reference and restoration dunes except for the young planted sites in Mae's Beach (See a. in Figure 4.3). Specifically, (1) *Dorymyrmex flavus* McCook and *Forelius pruinosus* (Roger) were the most common species in intact foredunes, but the abundance of *F. pruinosus* decreased in the degraded sites. (2) The dominant species shifted from *D. flavus* to *F. pruinosus* after dunes were re-built. (3) *Brachymyrmex patagonicus* Mayr, which is invasive, became the most numerous species in old planted sites. Disturbance also influenced the composition of functional groups (See c. in Figure 4.3). Dominant Invasives were present in degraded and restoration areas. In addition, Cryptic Species, which were only found in backdunes, appeared in degraded, old planted, and re-built sites.

Ant diversity was not different between before and shortly after oil pollution, but increased after three years (See a. in Figure 4.4). Ant communities in Grand Isle State Park were different between before and long after, and between shortly and long after, oil pollution. Ant communities in Port Fourchon were different between before and shortly after, and between before and long after pollution (Table 4.1, See b. in Figure 4.4). The number of ant functional groups increased after oil pollution in both locations (See c. in Figure 4.4).



	Intact
Degraded	0.0003

R=0.2439

	Planting (old)	Reference
Planting (young)	0.0001	0.0028
Planting (old)		0.0012

R=0.6737

	Re-built	Reference
Planting (young)	0.0001	0.0657
Re-built		0.0005

R=0.5577

Figure 4.3 **a** ANOSIM results between intact and degraded dunes, and between reference and restoration dunes. **b** Rényi diversity profiles, and **c** Functional group profiles of intact, degraded, reference and restoration dune.

Table 4.1 PERMANOVA results (F and P value) of the ant communities among before, shortly after, and long after oil pollution. * shows significant difference.

		F				P		
Grand Isle State Park		before	short	long		before	short	long
	before		0.737	5.23	before		0.665	0.009*
	short	0.737		3.78	short	0.665		0.027*
	long	5.23	3.78		long	0.009*	0.027*	
Port Fourchon	before		4.827	7.45	before		0.024*	0.009*
	short	4.827		2.32	short	0.024*		0.112
	long	7.45	2.32		long	0.009*	0.112	

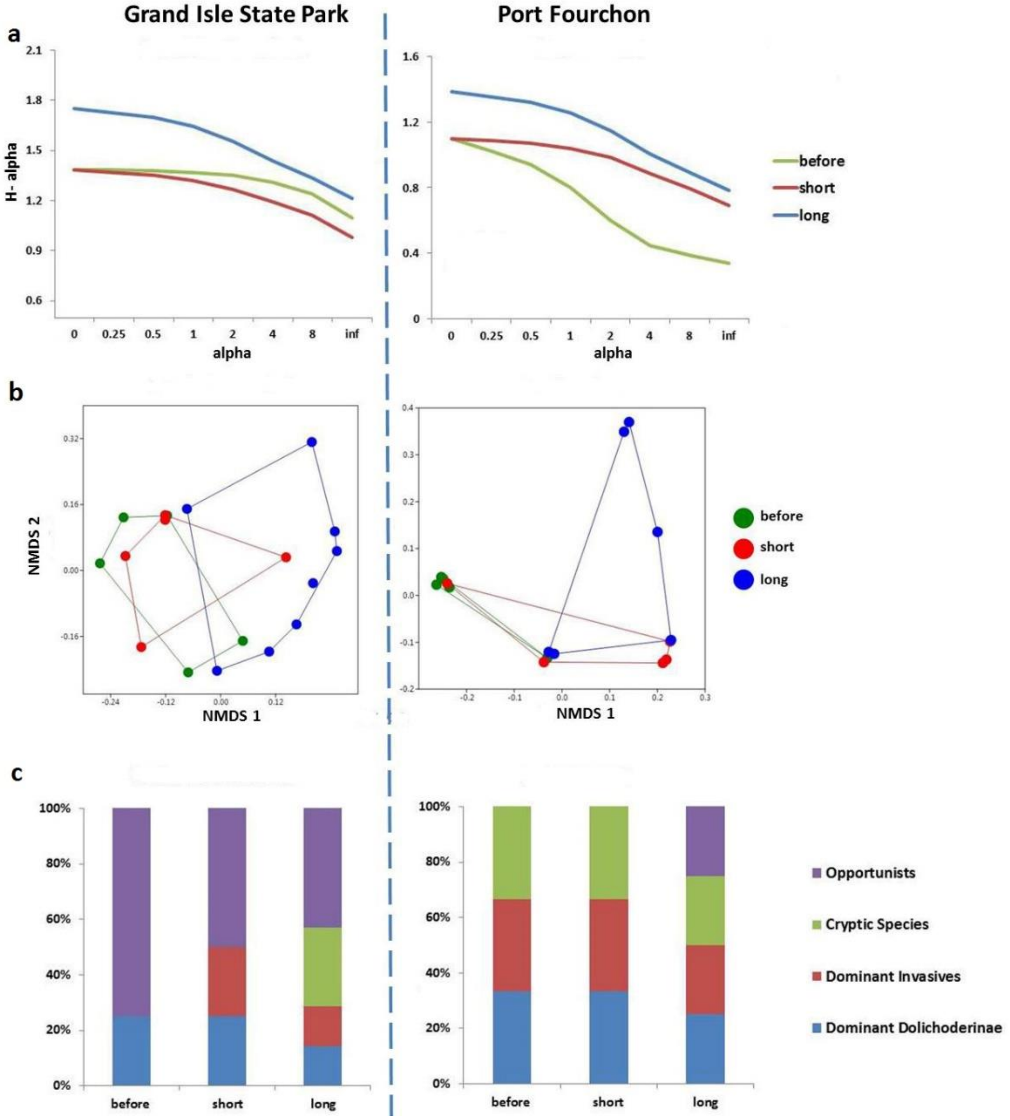


Figure 4.4 **a** Rényi results, **b** NMDS profiles, and **c** Functional group profiles of ant among before, shortly after, and long after oil polluted areas.

4.4 Discussion

Both taxonomic composition and functional groups respond to disturbance. *D. flavus* and *F. pruinosus* are the most common species in intact foredunes (Chapter 2). They are active in open sandy places and can forage on hot ground which may be too hot for other ants (Antweb.org; Valone and Kaspari 2005; Warriner *et al*. 2008). In disturbed areas, the population of one of these two species decreased depending upon the type of disturbance. Retrogression of primary succession can be caused by disturbance, which may be one explanation for the changes in the size of these ant populations (Kaufmann 2001). However, testing succession processes and hypotheses is beyond the scope of this paper. More information is needed to determine which one of these two species is the pioneer and how disturbance resets the ant succession on dunes.

The most obvious change of functional groups is the positive association between *Solenopsis invicta* Buren (Dominant Invasives) with disturbance. This is predictable because, when present, this species generally occurs in anthropogenically modified areas. In addition, the disappearance of Generalized Myrmicinae is also expected because this group is sensitive to disturbances (Gomez et al., 2003; Castracani et al. 2010). Although Cryptic Species have previously been shown to have a negative response to disturbance (Hoffmann and Andersen 2003), their wide occurrence in disturbed areas is not surprising. This is because the only species belonging to this group in foredunes is *Brachymyrmex patagonicus* Mayr, a ubiquitous, introduced species known nests close to urban areas (MacGown et al. 2007). The original hypothesis was that Opportunists act as a pioneer group that first colonize in the early succession stage such as the planted beach and re-built dunes, followed by Dominant Dolichderinae that are shown to increase in abundance in moderately disturbed areas (Andersen and Majer 2004). The results, however, don't support this expectation. More detailed research is needed not only to study the relationship between disturbance and functional groups, but also to test whether the responses found in this study are consistent in other dune habitats worldwide.

The sites in degraded dunes contain well-protected foredunes surrounded by areas of high human-mediated disturbance. Even though few anthropogenic disturbances occur directly on those foredunes, the ant community composition between intact and degraded foredunes is different. This is likely caused by species from the adjacent, disturbed environments entering the dunes and outcompeting native dune species or a loss of native dune species due to the loss of the slack and backdunes (Golden and Crist 2000; Crist 2009). In either circumstance, this research indicates the importance of (1) providing preservation areas large enough to encompass all habitats on the coastal dunes, and (2) reducing the isolation of dune habitats.

The planted grass can hold sand and trap windblown sediment, which are essential for building new dunes. There is a growing interest in evaluation of the recovery of biodiversity and ecosystem functions in restoration areas (Lamb et al. 2005). Most studies, however, focus on vegetation selection and monitoring the survival and growth of planted grass, and few mentioned how planting affects invertebrates. This research showed that the ant community changed in planted sites, which may be due to the change in vegetation structure (high plant cover and decreased plant diversity) caused by the monocultures of *P. amarum*. To determine more suitable planting strategies, such as using a variety of species instead of planting a single one, more studies are needed to detangle how planting activities affect other invertebrates as well as the whole dune ecosystem.

The changes of diversity, community structure, and functional groups of ants after three years of pollution is due to the occurrence of *Solenopsis molesta* Emery, *Nylanderia wojciki* (Trager), and *Pheidole moerens* Wheeler which were not found before the oil spill in Grand Isle

State Park. The appearance of *S. invicta* may be associated with beach cleaning activities after pollution (Tschinkel 2006), and *S. molesta* may follow the spread of *S. invicta* (Rao and Vinson 2004). *N. wojciki* can nest in sandy habitats (Kallal and LaPolla 2012), and was found in dunes in other areas (chapter 2). The reason it was not detected before oil pollution may be simply due to less intensive sampling. However, it is still not clear why *P. moerens* occurred three years after oil spill.

This study highlights the value of ants as indicators in coastal dune ecosystem because: (1) their diversity and occurrence is high in dune habitats, (2) they are easy to sample, and (3) both community composition and functional groups are sensitive to human disturbances, especially functional groups which are useful for assessing environmental changes in land management areas (Andersen et al. 2004; Narendra et al. 2011).

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CHAPTER 5. ANT DIVERSITY IN SALT MARSHES

5.1 Introduction

Salt marshes have a worldwide distribution (Pendleton et al. 2012). Although they only cover less than 0.01% of the earth's surface (Desender and Maelfait 1999), salt marshes perform critical ecological functions and have important economic values (Barbier et al. 2011, Vernberg 1993). Like other types of coastal ecosystems, however, salt marshes are under a variety of threats. The major stressors in the northern Gulf of Mexico include dredged canals, levee construction, land-use changes, subsidence, and sea level rise (Kolker et al. 2011, Shirley and Battaglia 2006, Turner 1997).

Insects constitute a large proportion of species richness and biomass and play significant roles in maintaining salt marsh health (Teal 1962). They can be used as bioindicators to evaluate how multiple disturbances affect the ecosystem (Petillon et al. 2008). However, few studies have focused on the diversity of insects in the salt marsh. The goal of this study was to uncover ant community structure in salt marsh Louisiana.

5.2 Methods

5.2.1 Study sites and sampling methods

Quadrat sampling was used to study ant abundance and community structure in two salt water marshes in July and August of 2010: Golden Meadow (29°18'45"N, 90°14'14"W) and LUMCON (29°16'27"N, 90°38'47"W). One transect in each site (containing 8 quadrats and separated by 10m) was set. In each quadrat, visible ants (foragers) were collected by using aspirators in the field. All *Spartina alterniflora* Loisel in the quadrat was then cut and brought to laboratory. The stems of *S. alterniflora* were checked individually to collect the ants nesting in the plant. Then, the vegetation information−fresh and dry weight, number of the maximum height of live and dead stem− was recorded.

Net sweeping was performed after quadrat sampling in order to generate more species: Two transects (20 meters long) paralleling to each other were set in each site that were separated by 30 meters. All insects collected by net were transferred to storage containers and stored in 95% ethanol solution. Ants were sorted from each container in the laboratory.

5.2.2 Data analysis

Multiple linear regression was used to determine the correlation between ant density (either foragers or all ants) and vegetation structure using SAS (PROC REG). Both backward and forward selections were used to determine the variable that affects ant community the most. Variables were log-transformed before analysis, if necessary, to ensure normal distribution.

5.3 Results

Only three ant species were found in the salt marsh: *Crematogaster pilosa* Emery, *Pseudomyrmex gracilis* (Fabricius), and *Camponotus impressus* (Roger). *C. pilosa* was the dominant species. The mean number of *C. pilosa* foragers was 16.1 ± 11.6 (SD)/ quadrat, and the total number of *C. pilosa* was 123.7±143 (SD) / quadrat. Only one or two individuals of *P. gracilis* were found in some quadrats. *C. impressus* was only sampled by net sweeping. In addition, no significant correlation was detected between ant density and vegetation factors.

5.4 Discussion

Ant diversity in the salt marsh is low compared to other coastal ecosystems (Ellison 2012, chapter 2, 6, 7). Additional sampling with multiple methods has not resulted in more species (Hooper-Bùi, Adams unpublished). One reason is that the marsh ground is flooded by salt water most of the year, which may restrict the colonization of many ant species (Marko et al.

2004). Although some ants are able to move to trees during flooding (Soares et al. 2013), no species has yet been found that can inhabit the salt marsh ground. Another reason of this low diversity is due to the simple habitat structure. *S. alterniflora* is the dominant plant in the salt marsh along the northern Gulf of Mexico. *Juncus roemerianus* Scheele occasionally occurs in some places (Visser et al. 1998). Both *S. alterniflora* and *J. roemerianus* are herbaceous plants, and their physical structure is relatively simple. All three ant species were found living in the dead stems of *S. alterniflora*, and the hollow stems may be the only place that is suitable for building nests. Species richness has been documented that positively correlated with the complexity of habitat structure in many systems (McCoy and Bell 1991). As a result, it is not surprising that the simple marsh structure cannot support many ant species is not a surprise. The third reason for low ant diversity may be because of the behavior of *C. pilosa*. Although *Camponotus* belongs to Subordinate Camponotini and can show dominant behavior when Dominant Dolichoderinae absent (Andersen 1995), this is not the case in North America where *Camponotus* shows lower behavioral dominance than *Crematogaster* (Andersen 1997). The third species, *P. gracilis*, may have the lowest behavioral dominance (personal observation). *Crematogaster* not only dominates in salt marsh, but also can be aggressive in many other habitats (Adgaba et al. 2014, Marlier et al 2004, Tschinkel and Hess 1999). This may repel the colonization of other ant species.

No vegetation information recorded in this study was significantly detected that affects the density of *C. pilosa*. This was consistent with the result of Childress and Koning’s (2013) study who found only plant cover influences ants in the salt marsh. This may be due to the high frequency of disturbances which dilute the relationship between ants and the environment

(Brandt et al 2010). It is worth noting, however, that only 16 quadrats were analyzed in this study. More data are needed to acquire more solid conclusions.

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CHAPTER 6. HOW DO CHANGES OF HABITAT STRUCTURE BY MULTIPLE INVASIVE WOODY SPECIES AFFECT ANT COMMUNITIES IN FLOATING MARSHES?

6.1 Introduction

One of the oldest, but still not fully resolved, questions in ecology is what causes changes of communities across landscapes. Although the underlying mechanisms are undoubtedly complex, one explanation is that habitat structure — defined as the amount, composition and three-dimensional arrangement of (a)biotic physical matter (McCoy and Bell 1991) — plays a significant role in determining the species diversity and composition in both local and regional scale. What seems like an intuitional and straightforward mechanism, however, is much more complex. In addition, the habitat structure is currently gaining more attention because human activities have modified, and will continually alter, the habitat configurations (Soulé and Orians 2001). One representative example is biological invasion.

Biological invasion has been recognized as one of the major threats to the integrity and functionality of ecosystems (Vitousek 1990). It is still not fully understood, however, how invasive species affect communities. For example, instead of decreasing diversity, a few studies indicated that exotic species (especially plants) can increase the heterogeneity of the ecosystem, leading to higher diversity and/or distinct species composition (e.g., Petillon et al. 2010). In addition, how multiple invasions affect the community structure and functions is still unclear, especially in wetlands (Groshol 2002). Elucidating the relationship between habitat structure and invasive species will make an enormous contribution to conservation activities. Here, I studied how changes of habitat structure by multiple invasive woody plant species affect ant communities in floating marshes.

Floating marshes (flotant) occur extensively only in a few locations in the world, including the Danube Delta, the floodplains of the Nile and Amazon River, and the Mississippi River Delta (Swarzenski et al. 1991). They are unique wetland type in that the marsh surface is rarely if ever flooded (Sasser et al. 1996).The herbaceous species (such as *Panicum hemitomon* Schult.) are rooted in highly organic buoyant mats (Figure 6.1, habitat 1). The mat rises and falls with changes in water level, keeping the surface of these marshes dry at all times (Swarzenski et al. 1991). Without flooding stress, floating marshes may support animal life that cannot survive in other types of wetlands. In addition, those marshes perform valuable ecological functions such as providing habitats for many species and protecting coastlines from storm and wave action (Battaglia et al. 2007). Like other coastal wetlands, however, floating marshes are affected by anthropogenic and natural disturbances such as canal and levee building, hurricanes and associated storm surge, water fluctuation, and invasive species (Turner 1997).

The invasive processes in floating marshes of Louisiana are quite interesting. First, since the surface of flotant is free from inundation, the native less flood-tolerant shrub wax myrtle (*Morella cerifera* (L.)) invades the marsh and becomes the dominant species in some places with thick mats (Figure 6.1, habitat 2). Then the establishment of wax myrtle has facilitative effects on the spread of another woody species — Chinese tallow (*Triadica sebifera* (L.)), which invaded the US in the late 1700s from Asia (Figure 6.1, habitat 3). These two woody species act together as ecosystem engineers and change the understory micro-climate, which benefits the invasion of some exotic grasses (Battaglia et al. 2009). The multiple invasion changes floating marshes greatly: from herb dominant to herb-bush-tree systems. These various habitats occur in a relatively small area, which enables one to focus on how changed habitat structure modifies the species assemblages while minimizing the confounding effects of climate, soil, and biogeographic history. Given these interesting multiple invasion processes, it is surprising that only two studies (Battaglia et al. 2007, 2009) mentioned the effects of invasion on vegetation, and to my knowledge, no research has yet examined how this invasion process influences other trophic levels such as insects.

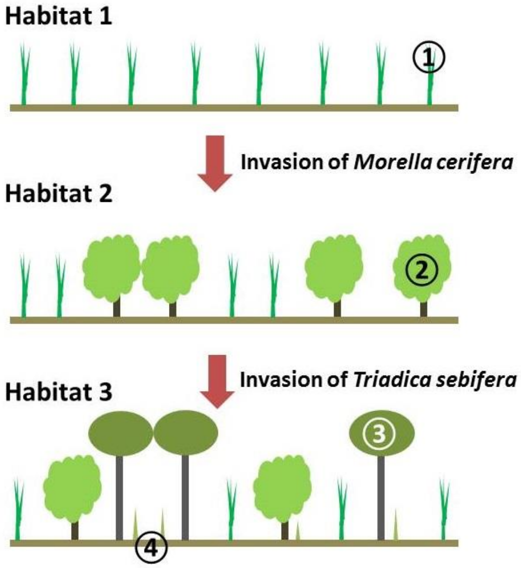

Figure 6.1 Schematic representation of the process of multiple invasion by woody species in floating marsh in Louisiana. ① *Panicum hemitomon* Schult; ②*Morella cerifera* (L.); ③*Triadica sebifera* (L.); ④ invasive herb.

Insects, which play important ecological roles in ecosystem, are largely unstudied in wetlands. Insects constitute a substantial proportion of species richness and biomass, and play significant roles in controlling and maintaining processes which are essential for the function of ecosystems such as stabilizing food webs and nitrogen cycling (Weisser and Siemann 2004). However, complete inventories of all insects in one habitat present a challenge due to the limitations of time, money, and taxonomic knowledge. A widely used alternative is to survey bio-indicators. Ants are one of the most widely used insect indicators because they are sensitive to habitat modifications and respond to the changes in ways similar to other animals and plants

(Agosti et al. 2000). These makes ants a powerful environmental monitoring tool for future conservation programs.

The hypothesis of this study is: multiple invasions by woody species will change the diversity, community structure, and functional groups of ants in floating marshes. Before invasion, the floating marshes were dominated by one or two herbs whose leaf surface and hollow stems can only provide limited nesting and foraging sites for ants. The invasive woody plants may relieve this environmental filter by increasing the habitat complexity and heterogeneity, which may lead to higher diversity and alternative species composition.

6.2 Methods

6.2.1 Study sites and sampling methods

Ants were sampled in two sites (FM4 and Morone) in the floating marsh of Jean Lafitte National Historical Park and Preserve in July and September, 2015. Hand collecting was used because the large variation of vegetation structure among habitats. Five plots were set in each site in the non-invasive area. Hand collecting was performed in each plot for ten minutes to sample all ants that were found on the grass and mat. Three to six wax myrtle and Chinese tallow were randomly selected in invasive areas. Ants were sampled for ten minutes near the root, on the trunk, and in the canopy, respectively. All ants were collected by using aspirators, and stored in 95 % ethanol, and later identified to the species level in the laboratory.

6.2.2 Data analysis

Data from root, trunk, and canopy was pooled to represent the species composition of each woody plant species. Richness was compared between invasive and non-invasive areas using analysis of variance (ANOVA) in SAS 9.3 (PROC GLIMMIX). Rényi diversity profiles were performed to study the differences of diversity between different plants. Ant species were also assigned to functional groups as described by Andersen (1997) and Hoffmann and Anderson (2003). The patterns of ant composition were investigated using non-metric multidimensional scaling (NMDS) and one-way Permutational Multivariate Analysis of Variance (PERMANOVA) using PAST (Hammer et al. 2001).

6.3 Results

A total of 96 individuals representing 12 species, eight genera, and four subfamilies were found (Table 6.1). The most common species in both grass and woody places was *Crematogaster pilosa* Emery. The rare species represented by only one individual were *Solenopsis molesta* Emery, *Pseudomyrmex gracilis* (Fabricius), and *Myrmecina americana* Emery. The Rényi profiles showed that wax myrtle supported the highest ant diversity, and the grass areas had the lowest diversity, ant diversity in tallow was not different from that in myrtle and grass (Figure 6.2).

Table 6.1 Functional groups with assigned ant species. Information of each species is provided on its occurred habitat.

Functional Group	Species	grass	myrtle	tallow
Subordinate Camponotini	*Camponotus impressus*			X
Generalized Myrmicinae	*Crematogaster pilosa*	X	X	X
	Pheidole dentata		X	X
Tropical Climate Specialists	*Pseudomyrmex pallidus*	X	X	X
	Pseudomyrmex gracilis		X	
Cold Climate Specialists	*Myrmecina americana*		X	
Opportunists	*Aphaenogaster f-r-t* group		X	X
	Solenopsis molesta			X
Cryptic Species	*Hypoponera opaciceps*	X	X	X
	Pheidole moerens		X	
	Pheidole floridana			X
	Solenopsis picta			X

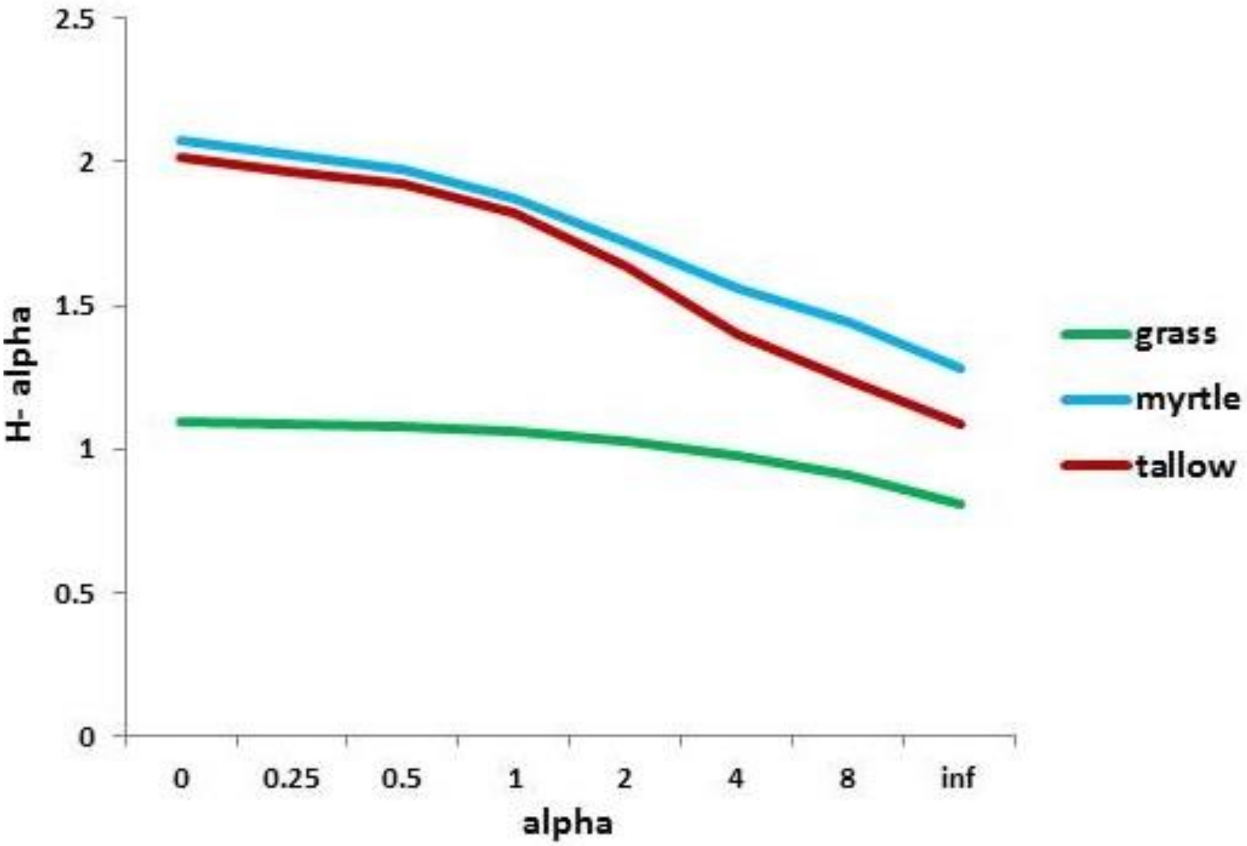

Figure 6.2 Rényi profiles for ant diversity in different plants of the floating marsh in Jean Lafitte National Historical Park and Preserve.

Six of nine functional groups defined by Andersen (1995) were found. Dominant Dolichoderinae, Hot Climate Specialists, and Specialist Predators was not found here. Generalized Myrmicinae, Tropical Climate Specialists, and Cryptic Species were detected in all areas. Cold Climate Specialists and Subordinate Camponotini were only collected in the myrtle and tallow respectively (Figure 6.3). Grass supported the lowest diversity of functional groups, and myrtle had more functional groups compared the others.

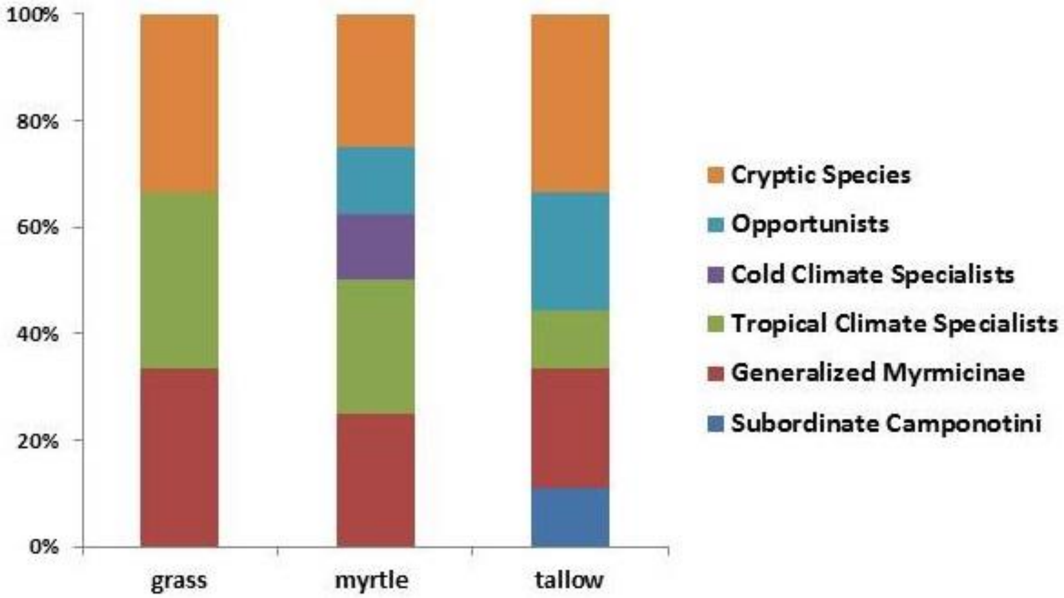

Figure 6.3 Functional group profiles of floating marsh ants in different plants. Data are relative contributions of each functional group to total species richness.

NMDS graph showed that the plots of grass, myrtle, and tallow overlapped (Figure 6.4). The results of one-way PERMANOVA further confirmed that the community structure in the three type of plants was similar (Total sum of squares = 2.393, Within-group sum of squares = 2.098, F = 1.197, P = 0.3409).

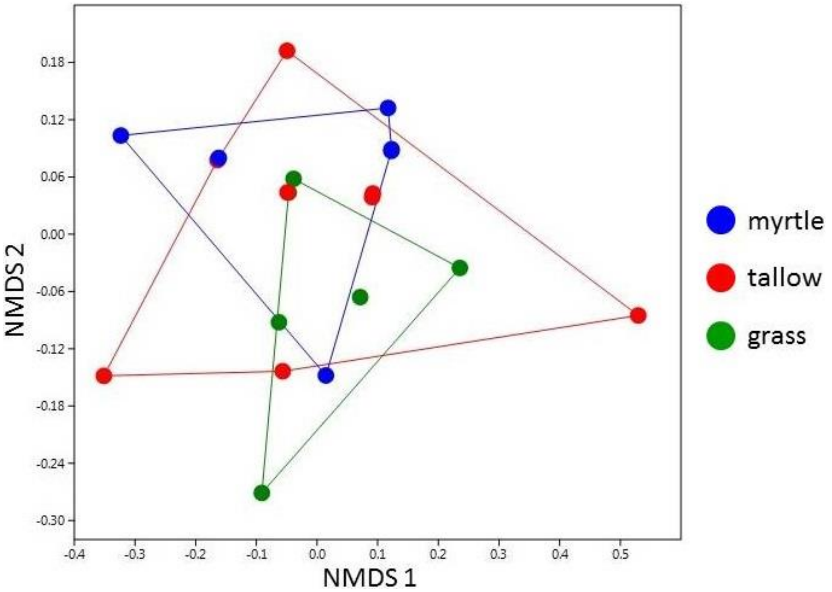

Figure 6.4 non-metric multidimensional scaling (NMDS) for ant species composition in different types of plants in floating marsh.

6.4 Discussion

The invasive plants, wax myrtle and Chinese tallow, supported more species of ants than that in non-invasive areas. Ant species in the grass areas is a subset of those in invasive places. This may be because the woody species provided more niches than grasses for ant nesting and foraging. For example, *Camponotus impressus* (Roger) and *Solenopsis picta* Emery were commonly collected in the twigs (AntWeb.org). In addition, some species, such as *Aphaenogaster f-r-t* group and *M. americana*, were exclusively collected at the root area of bushes and trees. Whether these species nest in the root area which is less flooded or in the lower part of the trunk is still not clear. More data are needed to reach a solid conclusion about this point.

Three functional groups— Dominant Dolichonderinae, Hot Climate Specialists, and Specialist Predator— were not found in the floating marsh, which may be because of the unsuitable environment (Hot Climate Specialists prefer to live in dry but not high humidity areas like marsh) and/or lack of necessary resources (e.g., no hosts for parasite species like *Polyergus*) (Andersen 2007, Trager 2013).

No statistical significant difference of species composition was detected between grass and woody areas, or between the two woody species. However, the ecological difference was obvious between the invasive and non-invasive areas: three of the six functional groups could only be found in the bushes and trees. The species composition in grass is more like that in the salt marsh (see Chapter 5), and ant community structure in myrtle and tallow is nested of that in swamp (see Chapter 7).

This study supports the hypothesis that invasive species can act as ecosystem engineers, and can change the local diversity by modifying habitat structure (Crooks 2002). The invasion of myrtle and tallow adds a novel canopy layer and dryer root area in floating marsh, which not only increased the heterogeneity of physical structure, but also altered the light available under the woody species (Battaglia et al. 2007). The changed environmental factors may benefit the extension of some species which normally would not occur in the native system (Mendez et al 2015). Further study is needed to document if this invasion has similar effects on other organisms (Elleriis et al. 2015).

In Louisiana, three destructive invasive ant species that are likely to impact the floating marsh in the near future. The red imported fire ant is present in some areas of the floating marsh in low numbers (Chen unpublished). Argentine ants (*Linepithema humile* (Mayr)) and tawny crazy ants (*Nylanderia fulva* (Forel)) form supercolonies and have the potential to radically change the floating marsh ecosystem, which may cause invasive meltdown (Simberloff 2006). The floating marsh that has been pre-invaded by the two woody plants may be preconditioned for the invasion of one or both of these ants.

It is worth noting that the sampling size of this study is quite small: less than ten collecting units (plot or tree) were sampled in only two locations. More units and locations are needed in future studies in order to reach more solid conclusions.

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CHAPTER 7. ANT ASSEMBLAGES AND CO-OCCURRENCE PATTERNS IN CYPRESS-TUPELO SWAMPS

7.1 Introduction

Forested wetlands provide critical ecological and economic services at local and global scales (Mitsch and Gosselink 2007). Cypress and tupelo swamps, for example, are important components of coastal forested wetlands in the southeastern United States (Ewel and Odum 1984), and perform multiple functions such as exporting organic debris, providing habitats for wildlife, and shoreline protection (Lowery 1974, Doyle et al. 1995, White et al. 2001, Gooding and Langford 2004). Unfortunately, these areas are among the most rapidly vanishing ecosystems because of logging, saltwater intrusion, sinking and subsidence, defoliation, and little regeneration (Effler and Goyer 2006, Hoeppner et al. 2008, Faulkner et al. 2009, Shaffer et al. 2009). Additionally, these problems are intensified by global sea level rise, hurricanes, and invasive species (Pezeshki et al. 1987, Conner et al. 2002, 2014). major gaps still remain in the knowledge of insect diversity and community structure in these wetlands (Sklar 1985, Parys et al. 2013).

Ants (Hymenoptera: Formicidae) are among the most diverse insect groups, and play important ecological functions in forests such as stabilizing of food webs and influencing the composition of other organisms (Hölldobler and Wilson 1990, Folgarait 1998, Hess and James 1998, Floren et al. 2002, Davidson et al. 2003, Philpott and Armbrecht 2006, Koch et al. 2011, Tanaka and Itioka 2011, Mestre et al. 2012). In addition, ants are suitable bioindicators to evaluate how disturbances (natural and/or anthropogenic) affect forest ecosystems because they are sensitive to habitat changes, act as surrogates of the diversity of other organisms, have a well-established taxonomic base, and are relatively easy to sample (Oliver and Beattie 1996a, 1996b, Agosti et al. 2000, Floren et al. 2001, Andersen and Majer 2004, Schonberg et al. 2004, Widodo et al. 2004, Underwood and Fisher 2006, Leal et al. 2010). Ants, however, have received much less attention in swamps than in other types of forests (but see Tagwireyi and Sullivan 2015).

Studies in other types of forests indicated that the canopy can support high ant diversity (Wilson 1987, Floren and Linsenmaier 2001, 2005), and the diversity and community structure of ants differs along vertical strata (Tschinkel and Hess 1999, Yanoviak and Kaspari 2000, Tanaka et al. 2010, Neves et al. 2013). In addition, developmental stages, forest type, disturbance, and management strategies all influence ant composition (Schulz and Wagner 2002, Watt et al. 2002, Fonseca and Benson 2003, Bos et al. 2007). Moreover, canopy ants can show a mosaic pattern in simple forests: dominant species show exclusive distribution because of resource competition, and always co-occur with certain submissive species (Blüthgen et al. 2007). Many of those studies were carried out in tropical primary - and agricultural forests, and how ant species organize in swamps and other wetland forests remains unclear. Given that the soil of cypress and tupelo swamps is flooded throughout the growing season except during extreme drought, ants can only live in the canopy, trunk, and occasionally in the higher root areas. This provides an ideal system to study arboreal (tree-dwelling) ants without the interruption of ants nesting in the ground and leaf litter.

The goal of this study was to describe the ant community structure in cypress and tupelo swamps. The following hypotheses were tested: (1) arboreal ant diversity is relatively lower in swamps than in other forests; (2) ant assemblages differ between habitat stratum: canopy vs trunk; (3) cypress, tupelo, and maple support distinct ant communities; and (4) ants show mosaic co-occurrence patterns in swamps. Because invasive red imported fire ants (*Solenopsis invicta* Buren) were sampled in one of my sites, I tested if fire ants affect ant composition or change the co-occurrence patterns in swamps (Kaspari 2000).

7.2 Methods

7.2.1 Study sites and sampling methods

Ants were sampled in three cypress and tupelo swamps in Louisiana: Jean Lafitte National Historical Park and Preserve, Maurepas Swamp Wildlife Management Area (Eastern Tract), and a swamp in the north shore of Lake Verret (Figure7.1). The swamps are composed of predominantly bald cypress, *Taxodium distichum* (L.) Rich, and water tupelo, *Nyssa aquatic* L. All of the sites are secondary forests and have not been harvested since the 1920’s. This region is characterized as a sub-tropical climate with an average annual rainfall of 1700 mm and temperature of 20°C.

	Cypress			Tupelo			Maple		
Year	2011	2012	2014	2011	2012	2014	2011	2012	2014
Jean Lafitte	3 (1)	6		3	3		3	3	
Maupreas	4	5 (1)		6 (1)	5		5	5 (2)	
Lake Verret			6 (5)			6 (6)			

Figure 7.1 Location of study sites (yellow square in the Gulf of Mexico map shows the area of study sites). **1** Jean Lafitte National Historical Park and Preserve, **2** Maurepas Swamp Wildlife Management Area, **3** Lake Verret swamp. The table shows number of each tree species that was selected in each year, and the parentheses indicate of trees at each site that were infested by invasive red imported fire ants.

Several cypress and tupelo (DBH > 25cm) in each swamp were randomly chosen between May and August of 2011, 2012, and 2014. In Jean Lafitte and Maurepas, several red maple, *Acer rubrum* L. *var. drummondii* (Hook. and Arn. Ex Nutt.) Sarg (DBH > 15cm) were selected, in addition to the cypress and tupelo because it was the dominant understory tree in those swamps. The distance between any selected tree was >50 meters, and each sampling area was >200 meters away from human construction such as roads, parking areas, and pipelines to minimize any edge effect.

Fogging and baiting, the most common collection methods used in canopy ant studies, were not suitable for this study. The National Park system forbids the use of fogging techniques which may compromise sensitive habitats, and the branch size of most trees was not thick enough to use the single rope technique (Perry 1978). As a result, two types of canopy traps (bottle and cup traps) were deployed using slingshots, and one trunk trap was tied around the trunk at breast height (1.4m) in each tree (Chen et al. 2012). Traps were filled with 15ml of ethylene glycol as a preservative and emptied at two-week intervals for a duration of eight weeks in Jean Lafitte and Maurepas, and six weeks in Lake Verret. Ants were sorted and preserved in 95% ethanol and identified to species. Ant species were then assigned to functional groups as described by Andersen (1997).

7.2.2 Data analysis

Rarefaction and extrapolation curves were generated to compare ant species richness between habitat stratum and among three tree species using EstimateS 9.1.0 (number of samples in maple was extrapolated to 24 based on Chao 2, Colwell 2013). Rényi diversity profiles were performed using Biodiversity R (Kindt and Coe 2005; R Core Team 2013) to study the differences of diversity between stratum and among tree species. The higher position of the line indicates higher diversity (Tóthmérész 1995; Kindt et al. 2006).

Two databases were created to analyze ant community structure because (1) invasive species could disassemble communities (Sanders et al. 2003, Lessard et al. 2009), and (2) red imported fire ants occurred in most trees in Lake Verret, but only at a couple trees in Jean Lafitte and Maurepas (Figure 7.1). Database 1 contained trees without fire ants in Jean Lafitte and Maurepas; database 2 was composed of the fire ant infested trees in Lake Verret. It is not suitable to study the influences of fire ants in swamps by comparing these two databases directly because the effects of fire ants and location cannot be separated in this study. Given that ant composition did not vary between years: (Permutational multivariate analysis of variance (PERMANOVA, Anderson 2001), F= 1.1727, df= 1, P= 0.2388), the data of 2011 and 2012 were pooled together for the following analysis.

a. Database 1: Differences in ant species and functional groups were tested across the factors of stratum, tree species, location, and all interaction terms using PERMANOVA, a Type I sums of squares, 9999 permutations, and a Monte Carlo permutation test. Location was treated as a random variable for all tests. Type I sums of squares were chosen because the hierarchical nature of the factors with strata occurring within trees that existed within locations (Clarke *et al* 2014). Similarity percentages (SIMPER) were computed to identify which ant species and/or functional groups contributed the most to any differences found in non-random terms from the PERMANOVA tests. Contributions to dissimilarity were limited to the first 50%. All statistical PERMANOVA and SIMPER analyses were performed in PRIMER version 6.1.14 including the PERMANOVA+ package version 1.0.4 (PRIMER-E Ltd, 2012).

C-score (Stone and Roberts, 1990) was used as an index to study species co-occurrence. C-score is the average number of checkerboard units for all species pairs in a community—species (row) × sample (column) matrix. EcoSim 7.0 was used to generate C-scores from 5000 randomized matrices. Fixed-fixed algorithm was applied because species were assumed different in their frequency of occupation trees, and trees are different in providing habitats for ants

(Tschinkel and Hess 1999, Gotelli 2000). If the observed C-score is significantly higher than the generated C-score, then the ants may be segregated; if significantly smaller, aggregated. The matrices of ant assemblages in the canopy of cypress, tupelo, and maple were constructed to assess the ant co-occurrence patterns in swamps. In order to detect the effects of dominant species and non-native species on the rest of the assemblages, the analysis was run again without the dominant and non-native species in the matrices (Sanders et al. 2007, Pfeiffer et al. 2008, Fayle et al. 2013).

b. Database 2: PERMANOVA and SIMPER were used to study the differences of species composition and functional groups between strata and tree species, and null models were generated using EcoSim to test for the species co-occurrence patterns in fire ant infested trees in trees in Lake Verret.

7.3 Results

Ants were detected in all sampled trees except one cypress tree in Maurepas. A total of 5487 individuals representing 21 species, 11 genera, and 5 subfamilies were collected. The richest collected subfamily was Myrmicinae. The most abundant species was *Crematogaster vermiculata* Emery. The most frequently-occurring species was *Solenopsis picta* Emery, and the rarest species (sampled less than three times) were *Solenopsis molesta* (Say), *Pyramica membranifera* (Emery), *Camponotus decipiens* Emery, *Tetramorium bicarinatum* (Nylander), *Discothyrea testacea* Roger, and *Strumigenys louisianae* Roger. Seven non-native species were detected. Table 7.1 provides the detailed list of ant occurrence in this study.

On average, each individual tree of cypress supported 5.5 ±1.96 (SD) ant species, tupelo 5.4 ± 1.83, and maple 5.9 ± 2.62. Rarefaction and extrapolation curves approached an asymptote for canopy and trunk, and for cypress and tupelo trees, but not for maple trees (Figure 7.2 see

Appendix C for confidence intervals and standard deviation). The Rényi profile showed that the crown of cypress supported more ant diversity than that of maple (See b. in Figure 7.3); the condition is opposite for the trunk (See c. in Figure 7.3). Generally, ants collected on the trunk were more diverse than those collected in canopy (See d. in Figure 7.3).

Seven functional groups were found. *S. invicta* was categorized in Dominant Invasives which was not included in Andersen's (1997) characterization; and placed *S. molesta* in Opportunists, *P. moerens* and *S. picta* in Cryptic Species based upon their biological characteristics such as body size and interactions behavior with other ants. Additionally, Cold Climate Specialists were not found on maples, and Opportunists were only sampled on the trunks. Table 7.1 and Figure 7.4 provide more detailed information on the composition of ant functional groups in each stratum of different tree species.

The ant composition differed between the canopy and the trunk in swamps (F = 24.427; DF = 1; p = 0.0016). Location (F = 9.4794; DF = 1; p = 0.0001) and the interaction between tree species and location (F = 1.7454; DF = 2; p = 0.0499) also significantly impacted composition. The functional groups showed differences between location (F = 19.102 DF = 1; p = 0.0001) and were due to the three-way interaction effects of location, tree species, and strata (F = 3.2556; DF = 2; p = 0.0067). SIMPER analyses revealed that *Ph. moerens* contributed the most to dissimilarities between the species composition in the canopy and on the trunk. A complete list of species that contributed to the first 50% of dissimilarity is located in Table 7.2.

Of the 21 species, only the three *Crematogaster* were categorized as dominant species. No non-random co-occurrence pattern was detected based on the C-score with a FF algorithm except for ant assemblages in the tupelo canopy, which showed an aggregated pattern (Table 7.3).

Table 7.1 Functional groups with assigned ant species and subfamily. Information of each species is provided on its occurred tree (cypress, tupelo, and maple), habitat strata (canopy and trunk), $^+$ indicates non-native species. GM: Generalized Myrmicinae, SC: Subordinate Camponotini, TCS: Tropical Climate Specialists, CCS: Cold Climate Specialists, OP: Opportunists, CS: Cryptic Species, DI: Dominant Invasives.

functional group	species	subfamily	cypress		tupelo		maple	
			canopy	trunk	canopy	trunk	canopy	trunk
GM	*Crematogaster ashmeadi*	Myrmicinae	X	X	X	X	X	X
	Crematogaster vermiculata	Myrmicinae	X	X	X	X	X	X
	Crematogaster pilosa	Myrmicinae	X	X	X	X		
	Pheidole dentata	Myrmicinae		X	X	X	X	X
SC	*Camponotus snellingi*	Formicinae	X	X	X	X	X	X
	Camponotus pennsylvanicus	Formicinae		X			X	X
	Camponotus impressus	Formicinae	X	X	X	X		X
	Camponotus decipiens	Formicinae		X				X
TCS	*Pseudomyrmex ejectus*	Pseudomyrmecinae	X	X	X	X	X	X
	Pseudomyrmex gracilis$^+$	Pseudomyrmecinae	X	X	X	X		X
CCS	*Temnothorax schaumii*	Myrmicinae	X	X		X		
OP	*Solenopsis molesta*	Myrmicinae						X
	Tetramorium bicarinatum$^+$	Myrmicinae				X		X
CS	*Pheidole moerens*$^+$	Myrmicinae	X	X	X	X	X	X
	Solenopsis picta	Myrmicinae	X	X	X	X	X	X
	Pyramica membranifera$^+$	Myrmicinae		X				X
	Pyramica epinotalis$^+$	Myrmicinae	X	X	X	X	X	X
	Strumigenys Louisianae	Myrmicinae				X	X	
	Hypoponera opaciceps$^+$	Ponerinae		X	X	X	X	X
	Discothyrea testacea	Proceratiinae						X
DI	*Solenopsis invicta*$^+$	Myrmicinae	X	X	X	X		X

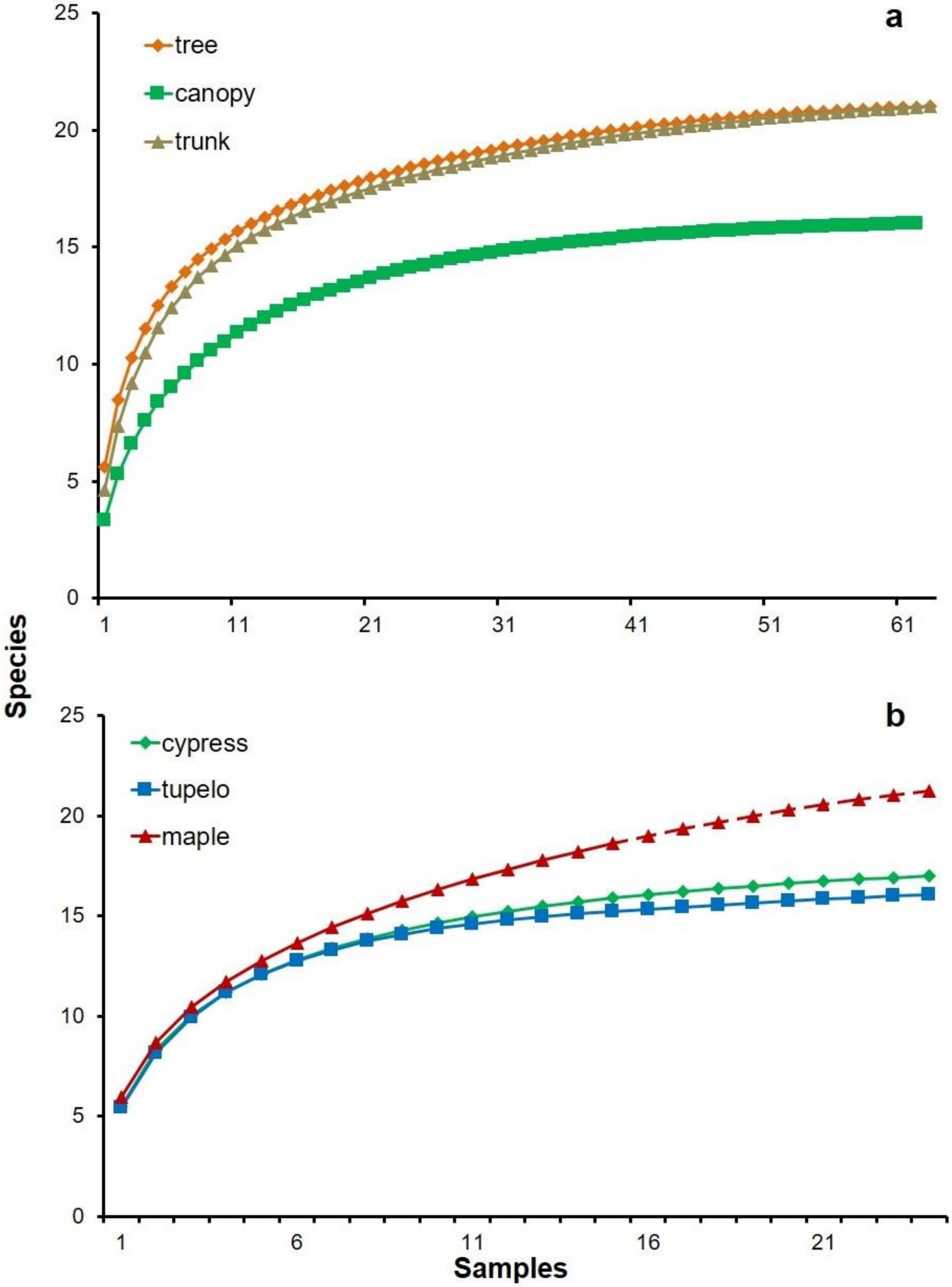

Figure 7.2 Sample based **(a)** rarefaction curves of different habitat strata (canopy and trunk), and **(b)** rarefaction (solid lines) and extrapolation (dashed lines) curves of different tree species (cypress, tupelo and maple). See Appendix C for confidence intervals and standard deviation.

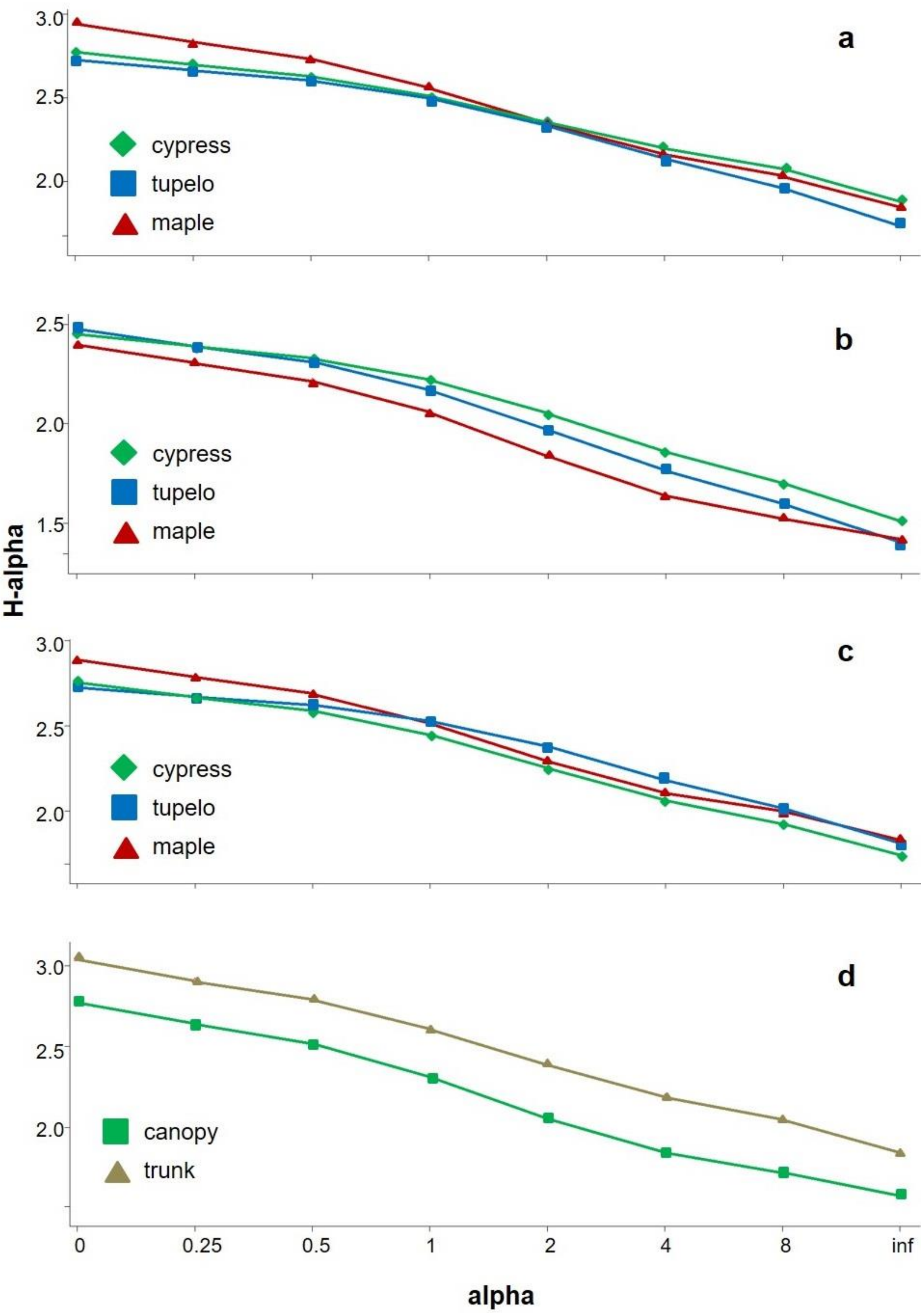

Figure 7.3 Rényi diversity profiles for ant diversity between **(a)** cypress, tupelo, and maple; **(b)** canopy and **(c)** trunk of different tree species, and **(d)** different habitat stratum in cypress and tupelo swamps.

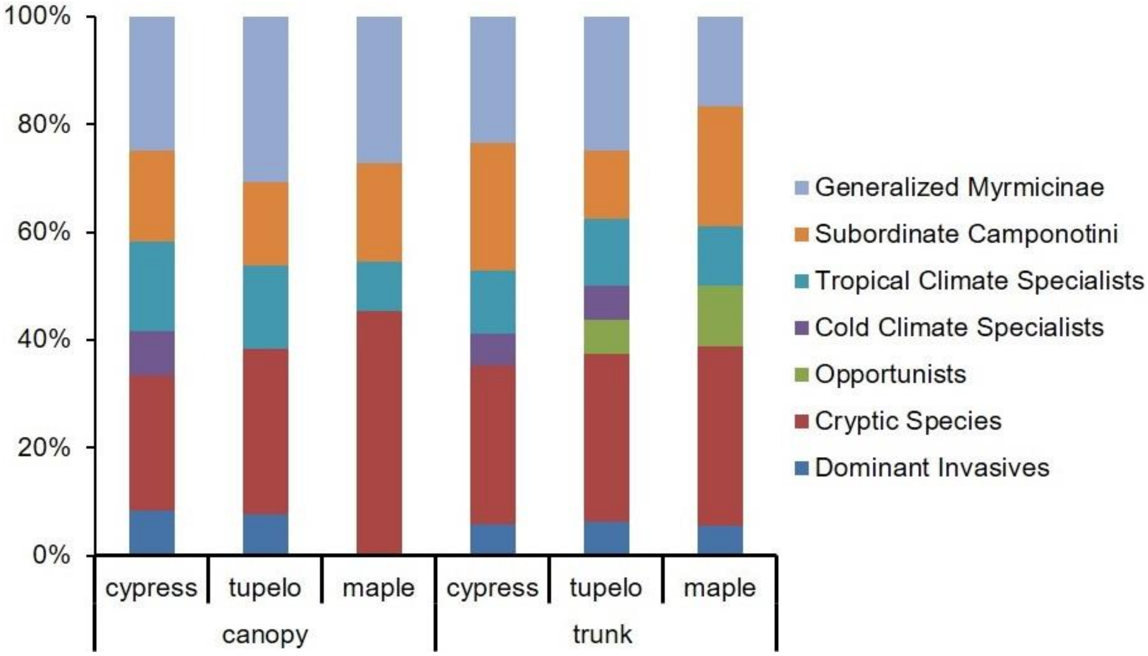

Figure 7.4 Functional group profiles of ant fauna from canopy and trunk of each tree species (cypress, tupelo, and maple). Data are relative contributions of each functional group to total species richness. Note that Opportunists only occurred in the truck of tupelo and maple, Dominant Invasives (fire ant *S. invicta*) was not detected in the canopy of maple.

Table 7.2 SIMPER analyses for the five ant species that contributed the most to dissimilarity between the canopy and trunk. Included are the average abundance in both the trunk and canopy (Trunk Avg. Abund, Canopy Avg. Abund), the average dissimilarity attributed to the ant species (Avg.Diss), standard deviation of dissimilarity (Diss/SD), and percent contribution (Contribution). Note that *S. picta* was the most frequently-occurring species in swamps, and *Pa. epinotalis* is a new record species in Louisiana (Chen et al. 2012).

Species	Trunk Avg. Abund	Canopy Avg. Abund	Avg. Diss	Diss/SD	Contribution
Ph. moerens	0.67	0.20	8.82	1.08	15.76
S. picta	0.65	0.76	7.13	0.79	12.74
C. ashmeadi	0.39	0.36	6.57	0.85	11.75
Ps. ejectus	0.26	0.29	5.21	0.77	9.32
Pa. epinotalis	0.28	0.22	4.90	0.73	8.75

Table 7.3 Observed, mean and variance of stimulated C-score, the probability of observed C-score smaller (o<s) and larger (o>s) than expected C-score based on null model, and Standardized effect size [SES = (observed C-score — stimulated mean C-score)/standard deviation of stimulated C-score] for ant community in the canopy of different tree species in each location, * indicates significant terms (α= 0.05).

Location	Tree species	community	Observed C-score	Mean of stimulated C-score	Variance of stimulated C-score	P (o<s)	P (o>s)	SES
Jean Lafitte	cypress	all species	2.6191	2.4198	0.0175	0.9486	0.1039	1.5047
		without dominants	2.7000	2.2809	0.0461	0.9638	0.0820	1.9511
		without non-native	2.4000	2.1169	0.0242	0.9710	0.1046	1.8208
	tupelo	all species	1.5357	1.6707	0.0058	0.0224*	0.9988	-1.7785
		without dominants	1.1333	1.2587	0.0045	0.0766	1.0000	-1.8609
		without non-native	1.1000	1.1765	0.0087	0.5812	1.0000	-0.8190
	maple	all species	0.6786	0.7480	0.0025	0.1214	1.0000	-1.3768
		without dominants	0.4667	0.5381	0.0033	0.1996	1.0000	-1.2484
		without non-native	0.4667	0.4667	0.0000	1.0000	1.0000	0.0000
Maurepas	cypress	all species	0.3000	0.3000	0.0000	1.0000	1.0000	0.0000
		without dominants	0.6667	0.6667	0.0000	1.0000	1.0000	0.0000
		without non-native	0.3333	0.3333	0.0000	1.0000	1.0000	0.0000

(Table 7.3 continued)

Location	Tree species	community	Observed C-score	Mean of stimulated C-score	Variance of stimulated C-score	P (o<s)	P (o>s)	SES
	tupelo	all species	1.3571	1.3358	0.0112	0.6428	0.5098	0.2024
		without dominants	0.8667	0.8294	0.0011	1.0000	0.4416	1.1244
		without non-native	1.4000	1.2377	0.0534	0.7734	0.2838	0.7027
	maple	all species	0.6944	0.7809	0.0193	0.6300	1.0000	-0.6218
		without dominants	1.0000	1.1302	0.0325	0.6194	1.0000	-0.7220
		without non-native	0.6786	0.7706	0.0326	0.7256	1.0000	-0.5096

Table 7.4 SIMPER analyses for the three ant functional groups that contributed the most to dissimilarity between tree species in Lake Verret swamp. Included are the average abundance in both the cypress and tupelo, the average dissimilarity attributed to the functional groups, standard deviation of dissimilarity, and percent contribution.

Functiona groups	Cypress Avg. Abund	Tupelo Avg. Abund	Av. Diss	Diss/SD	Contribution
Tropical Climate Specialists	0.60	1.00	8.37	1.13	23.55
Cryptic Species	1.10	1.42	8.13	1.13	22.87
Subordinate Camponotini	0.90	0.42	6.76	1.13	19.01

Crematogaster ashmeadi was the most abundant and frequently occurring species. *Pheidole dentata* and all rare species except *Py. membranifera* were not found when fire ants occurred. No significant difference of ant composition was detected between strata and tree species. Functional groups were different between cypress and tupelo (F = 3.9766; DF = 1; p = 0.0181), which was caused mainly by Tropical Climate Specialists (Table 7.4). No positive or negative species association was detected based on the analysis of EcoSim.

7.4 Discussion

7.4.1 Ant diversity in swamps

Swamps support less arboreal ant richness compared to other forest ecosystems, perhaps because the characteristics of the swamp limit the niche availability for ants. For example, (1) swamps in southeastern US have lower tree richness and fewer canopy layers. (2) Since major harvesting did not end until 1920s, most trees are relatively young, and their crowns are relatively small. (3) Some ants that nest in soil and leaf letter are a component of arboreal ant communities in many types of forests (Tschinkel and Hess 1999, Lubertazzi and Tschinkel 2003, Dolek et al. 2009). However, this is not the case in swamps because the ground is inundated most of the growing season and stays wet throughout the year. All of these suppositions may explain the lower ant diversity in swamps (Nielsen 2000, Ribas 2003, Campos et al. 2006, Ribas and Schoereder 2007). Directly comparing canopy ant diversity in different studies, however, is difficult and even unpractical, because of the inconsistent collecting methods—fogging, baiting, hand collecting, beating plants, trapping, fallen trees, observing. (Yanoviak and Kaspari 2000, Floren et al 2001, Ribas 2003, Gove et al 2005, Klimes 2012).

Three out of the nine ant functional groups were not sampled in swamps: Dominant Dolichoderinae (DD), Hot Climate Specialists (HCS), and Specialist Predators (SP). This result can be explained by: (1) the absence of nesting sites (e.g., *Forelius* (DD) nest in the ground), (2) an unsuitable climate (e.g., *Pogonomyrmex*, *Ephebomyrmex*, and *Myrmecocystus* (HCS) are typical desert ants which live in the arid habitats, Andersen 1997), and (3) a lack of food resources (e.g., *Polyergus* obligate parasites of *Formica* which was not found in swamp, Trager 2013).

7.4.2 Ant between strata (canopy vs. trunk) and among tree species (cypress, tupelo, and maple)

Most studies addressing ant stratification between strata focused mainly on canopy and ground (Bruhl et al. 1998, Yanoviak and Kaspari 2000, Vasconcelos and Vilhena 2006, Wilkie et al. 2010, Campos et al. 2011, Neves et al. 2013; but see Lubertazzi and Tschinkel 2003, Andersen et al. 2009, De la Mora et al. 2013), and showed that ant composition differed between those two habitats. The ant diversity and community structure here was different between canopy and trunk, which is not surprising given that the trunk has a different and much simpler morphological structure than the canopy. However, the data indicates that the trunk supported higher ant diversity, which is contrary to the results of previous studies (e.g., Tanaka et al. 2010). This may be because five rare species were only sampled on trunks. Among them, *S. molesta*, *T. bicarinatum*, *Py. membranifera*, and *D. testacea* can nest in rotting logs (Antweb.org); they may live in the fallen dead wood around the tree roots, and may not actually nest on the trunk. In addition, most canopy traps were only set on the larger branches diverging from the trunk in the lower canopy layers, which might have excluded ants living in the smaller branches and twigs of the upper crown (Tanaka et al. 2010, Janda and Konecna 2011). It is worth noting that this study only addresses ants occupying the lower canopy and trunk area is near the roots (trunk traps were set about 1.4m above the flooded ground). Future studies will be necessary to address the potential gradual change of ant composition from the top of the tree to the ground, given that the ant community and dominant assembly processes might not be the same in different layers of canopy and different parts of trunk (Hahn 2002, Hashimoto et al 2006, 2010, Ribeiro et al. 2013).

Although cypress, tupelo, and maple vary in a number of ways including surface rugosity, crown architecture, and leaf characteristics, no difference was detected in ant composition among the three tree species. One explanation is that the variability of tree structure may not influence arboreal ant communities in swamps. Furthermore, some ant species, such as *C. ashmeadi* and *Ps. ejectus*, are known to nest in a variety of trees across many habitats (Ward 1985, Tschinkel 2002, Dash 2004). Certain species that lack the exclusive requirement for nesting and foraging microhabitats may dilute any variance in ant composition among the different tree species. In addition, the study sites are secondary forests. The ant community may not show the difference among trees until the late recovery stages (Klimes et al 2012).

Compared with species, ant functional groups did not differ between strata. Andersen's functional group scheme categorized genus- and species-groups based on their responses to environmental stress and disturbance (Andersen 1995). Although the morphological features are different between the canopy and trunk, ants living in these habitats may face similar stress (Hood and Tschinkel 1990). It is noteworthy that the functional group scheme was not designed for local scale research (although it is very useful for studying human disturbance at particular sites, Hoffmann and Andersen, 2003).

7.4.3 Ant mosaics in swamps

The ant mosaic concept states that dominant ant species tend not to occur in the same patch because of the intra- and/or interspecific competition for resources. This is a popular hypothesis used to explain ant distribution patterns in canopies for the last 40 years (Leston 1973). Many studies have found the existence of mosaic patterns to be more prominent in secondary, agricultural, or other simple forests (Adams 1994, Dejean et al. 1994, Floren and Linsenmair 2000, Sanders et al 2007, Pfeiffer et al. 2008, Fayle et al. 2013). Although the study sites are secondary swamps dominated by only two or three tree species, few segregated or aggregated patterns were detected based on null models. In addition, when dominant or non-native species were eliminated from the analysis, the ant co-occurrence did not differ from the random pattern. Competition for stable food (especially with high carbohydrates) and/or shelter - that is easy to monopolize - is assumed to be the underlying mechanism leading to ant mutually exclusive and mosaic patterns (Hölldobler and Lumsden 1980, Jackson 1984, Blüthgen et al. 2004; but see Ribas and Schoereder 2002 and Sanders et al 2007). However, few insects that produce honeydew (aphids, coccids, or other homoptera insects) were collected in the samples. To my knowledge, cypress, tupelo, and maple do not continuously secrete any kind of nectar, or have any special morphological structure (e.g., domatium) for ant nesting. The absence of stable food and shelter resources may be the reason for lack of ant mosaics in swamps. Another explanation for non-detectable ant mosaics is that most of the canopy traps were set in the middle and lower crown due to limitations of the technique used here. The mosaics pattern may only exist in the higher canopy, which was not examined in this study (Ribeiro et al. 2013).

It should be noted that: (1) using co-occurrence patterns to infer species interaction is an indirect method. In order to make a solid conclusion, more information about ant life history, foraging behavior, colonization abilities, plus manipulative research and detailed colony mapping are needed (Floren and Linsenmair 2000, Ribas and Schoereder 2002, Blüthgen and Stork 2007). (2) Although few positive and negative associations were detected, this does not necessarily mean that dominant species (*Crematogaster* spp.) have no influence on ant community structure, or that species distribute randomly in the swamps. Competitive exclusion may exist but be too weak to detect, or does not lead to mosaic patterns, or be hard to prove due to the sampling methods.

7.4.4. Fire ants

Red imported fire ants, one of the most globally successful invasive species (Lowe et al. 2004), have invaded all states bordering the Gulf of Mexico. They are common in human disturbed areas (but can also be sampled in natural habitats, King and Tschinkel 2013), and have long been credited to be a major threat to local biodiversity (Wojcik et al. 2001). Although previously found in Louisiana swamps (pers. comm. Gregg Henderson, LSU), no one to my knowledge, has studied their influence on this ecosystem. Since fire ants were almost exclusively sampled in Lake Verret (creating a location effect), plus the lack of pre-invasion data, the effect of fire ants on ant assemblages cannot be studied directly. However, some phenomena may be related to the infestation.

First, *C. pilosa*, the dominant ant in the tidal salt marsh in southeastern US (Davis and Gray 1966, McCoy and Rey 1987, Childress and Koning, 2013), was only found in Lake Verret. In addition, *C. vermiculata* is the most numerous species in Jean Lafitte and Maurepas, but *C. ashmeadi* in Lake Verret. The changes in dominant species may be related to the occurrence of fire ants, given that invasive species have the potential to change or even dissemble native ant communities (Sanders et al. 2003). Second, *Ph. dentata*, a common species in both Jean Lafitte and Maurepas, was not sampled in Lake Verret. This could be due to the fact that *Ph. dentata* and *S. invicta* are known to show aggression toward each other, where the outcome is determined by colony size (Wilson 1976, Jones and Phillips 1990, Rao and Vinson 2004, 2009). In the infested swamp, the disappearance of *Ph. dentata* may be caused by the competition with fire ants, which can build large colonies (Chen unpubl. data). Third, whereas some of my data suggested that fire ants might influence ant assemblages in swamps, the common species and functional groups still occurred in infested area. Although most rare species were not sampled in Lake Verret, this may simply be due to the low activity of those species. In addition, no change of species co-occurrence pattern was detected. Swamps may be a poor environment for most ants. The low habitat quality can alter the species competition (Gibb 2011, King and Tschinkel 2013). In addition, the fire ant itself may not be a superior competitor that causes the decreased diversity in swamp (King and Tschinkel 2006, MacGown and Brown 2006, King and Tschinkel 2008, Menzel and Nebeker 2008, LeBrun et al. 2012). However, it is not the intention to uncover the effects of fire ants in this study. It is still early to make a robust conclusion without long-term monitoring and more replication of sites.

7.5 References

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CHAPTER 8. CONCLUSIONS

Inventorying ants that live in several coastal habitats is the first accomplishment of this dissertation. A species list, which serves as baseline data, is not only valuable for taxonomy studies, but also important for conservation and ecological research. To my knowledge, this is the first systematic study that addresses ant diversity in multiple coastal habitats. In total, 46 and 22 species were found in coastal dunes and wetlands, respectively. Although the diversity is relatively lower than that in many other ecosystems, most Andersen's functional groups were found.

The second part of this dissertation elucidated the changes of ant species composition along coastal gradients. In dunes, the bush areas supported a distinct ant community compared to other habitats (foredune, slack, and backdune), which is due to the lower species overlap between leaf litter and sandy ground (Clementsian pattern). In wetlands, most ants living in marshes can be found in swamps, which indicates a nested distribution pattern.

Then the project moved to uncover the niched-based mechanisms that drive ant assemblages. I focused on the roles of plant and ant interspecific competition, which were upheld as main factors that affected ant communities in many ecosystems. Not surprisingly, the dramatic changes of plant physical structure (grass to woody species) correlated with changes in ant diversity and composition. However, the vegetation appeared to have a small effect on ants within each type of habitat. The species interaction was also weak in dunes and wetlands.

I further elucidated the changes of assemblage processes along environmental gradients in coastal dunes. The analysis showed that deterministic processes dominated in the sandy habitats. Because vegetation and interspecific interaction had little effect on ants, overall abiotic factors, such as sand burying and desiccation, are presumed to determine ant composition. Under the bush, which provides a relatively suitable environment for ants because of the presence of leaf litter, the contribution of stochastic processes increased.

The last part of this dissertation addressed whether ants can be used as biological indicators in coastal areas. I found the response of ant communities to disturbances were condition dependent. Contrary to some studies, the diversity did not decrease, which may be because of the invasion of some exotic species such as *Solenopsis invicta* Buren. Disturbances, however, changed ant community structure and the composition of functional groups. This project supported the idea that ants are sensitive to both natural and human disturbances, and indicated that they are suitable bioindicators in coastal dunes and wetlands.

This project laid some ground-work in the field of insect ecology in the coastal areas. There remain, however, many aspects that are unexplored. First, this study did not cover all types of coastal habitats in the northern Gulf of Mexico because of the limited time and funding resources. For example, ants were only sampled briefly in a bottomland hardwood forest which is occasionally flooded. Examining how flooding affects ant communities of not only ground-dwelling, but also arboreal ants would be an interesting follow up study. Second, note that the metacomunity structure depends on the scale and geographical range of the study. If other habitats were included in the analysis, then the results may have been different. For example, nearly 10% of swamp ants were not collected in bottomland hardwood forests and 40% were not found in longleaf pine savannas. The ant distribution pattern may have been either Clementsian or Gleasonian if I only focused on coastal forests, and possibly nested if I addressed the spatial scale as the whole of Louisiana because all ants living in the coastal wetlands also have been found in inland ecosystems based on Dash’s thesis. Third, the underlying mechanisms were inferred from species distribution patterns in this project. Experimental study and field observations are needed to gather direct evidence of species interaction (such as competition) and the effects of environments (e.g., flooding and sand burying). Forth, ants are the only insect group addressed in this study. whether other insects respond to the environmental gradients the same way as ants in the coastal ecosystems is unclear. Lastly, this project only focused on the correlation between community taxonomic structure and disturbances. Application of functional traits have been demonstrated as an alternative and possibly a more reliable way to evaluate the effects of multiple disturbances. Future studies may apply these functional traits to gain a more complete picture of how communities respond to disturbances.

APPENDIX A. SUPPLEMENTARY MATERIAL FOR CHAPTER 2

A.1 Confidence Intervals (CI) and Standard Deviation (SD) of sample based rarefaction and extrapolation curves of the four habitats based on an average of series of 1,000 randomizations of the data. S: sample; S_{est}: observed number of species; LB: 95% CI Lower Bound; UB: 95% CI Upper Bound.

S	Foredune				Slack				Backdune				Bush			
	S_{est}	LB	UB	SD	S_{est}	LB	UB	SD	S_{est}	LB	UB	SD	S_{est}	LB	UB	SD
1	1.53	0.3	2.76	0.63	1.67	0.39	2.95	0.65	1.9	0.42	3.39	0.76	6.31	4.29	8.32	1.03
2	2.32	0.81	3.83	0.77	2.54	0.84	4.25	0.87	3.08	0.89	5.27	1.12	10.78	7.68	13.88	1.58
3	2.85	1.31	4.39	0.79	3.08	1.23	4.93	0.94	3.86	1.32	6.41	1.3	14.11	10.37	17.85	1.91
4	3.26	1.76	4.77	0.77	3.46	1.57	5.36	0.97	4.45	1.71	7.19	1.4	16.7	12.56	20.84	2.11
5	3.61	2.16	5.06	0.74	3.76	1.85	5.67	0.97	4.92	2.05	7.79	1.46	18.78	14.39	23.16	2.24
6	3.91	2.53	5.3	0.71	4	2.09	5.92	0.98	5.32	2.36	8.29	1.51	20.49	15.95	25.03	2.31
7	4.19	2.87	5.5	0.67	4.21	2.3	6.12	0.97	5.68	2.64	8.73	1.55	21.94	17.31	26.56	2.36
8	4.43	3.17	5.68	0.64	4.39	2.49	6.3	0.97	6.02	2.91	9.14	1.59	23.18	18.51	27.85	2.38
9	4.63	3.43	5.83	0.61	4.55	2.66	6.44	0.96	6.3	3.13	9.48	1.62	24.27	19.59	28.96	2.39
10	4.83	3.67	5.98	0.59	4.69	2.82	6.56	0.96	6.58	3.35	9.81	1.65	25.25	20.57	29.92	2.39
11	5.01	3.89	6.12	0.57	4.83	2.98	6.68	0.94	6.84	3.55	10.13	1.68	26.13	21.47	30.78	2.38
12	5.17	4.09	6.24	0.55	4.93	3.1	6.77	0.93	7.09	3.74	10.44	1.71	26.93	22.3	31.56	2.36
13	5.31	4.27	6.35	0.53	5.04	3.23	6.85	0.92	7.33	3.92	10.74	1.74	27.67	23.07	32.27	2.35
14	5.44	4.43	6.45	0.52	5.14	3.35	6.93	0.91	7.56	4.09	11.03	1.77	28.36	23.8	32.93	2.33
15	5.56	4.57	6.55	0.51	5.24	3.47	7	0.9	7.78	4.25	11.32	1.8	29.01	24.48	33.54	2.31
16	5.66	4.69	6.63	0.5	5.33	3.58	7.08	0.89	8	4.4	11.6	1.84	29.62	25.12	34.12	2.29
17	5.75	4.79	6.71	0.49	5.41	3.68	7.15	0.89	8.21	4.54	11.88	1.87	30.2	25.73	34.66	2.28
18	5.83	4.88	6.77	0.48	5.5	3.77	7.23	0.88	8.41	4.67	12.16	1.91	30.75	26.32	35.18	2.26
19	5.9	4.96	6.83	0.48	5.58	3.86	7.31	0.88	8.61	4.79	12.44	1.95	31.27	26.87	35.67	2.25
20	5.95	5.02	6.89	0.48	5.67	3.94	7.39	0.88	8.81	4.91	12.71	1.99	31.77	27.4	36.15	2.23
21	6	5.06	6.94	0.48	5.75	4.02	7.48	0.88	9	5.02	12.98	2.03	32.25	27.9	36.6	2.22
22	6.04	5.09	6.99	0.48	5.83	4.09	7.58	0.89	9.19	5.12	13.25	2.07	32.71	28.38	37.04	2.21
23	6.07	5.11	7.04	0.49	5.92	4.16	7.68	0.9	9.37	5.21	13.52	2.12	33.15	28.84	37.47	2.2
24	6.1	5.11	7.09	0.5	6	4.22	7.78	0.91	9.54	5.3	13.79	2.17	33.58	29.29	37.87	2.19

(A.1 continued)

S	Foredune				Slack				Backdune				Bush			
	S_{est}	LB	UB	SD	S_{est}	LB	UB	SD	S_{est}	LB	UB	SD	S_{est}	LB	UB	SD
25	6.12	5.11	7.13	0.52	6.08	4.27	7.89	0.92	9.72	5.38	14.06	2.21	33.99	29.71	38.27	2.18
26	6.14	5.1	7.18	0.53	6.15	4.31	7.99	0.94	9.88	5.45	14.32	2.26	34.38	30.11	38.65	2.18
27	6.16	5.09	7.22	0.54	6.21	4.34	8.09	0.96	10.05	5.51	14.58	2.31	34.76	30.5	39.02	2.17
28	6.17	5.08	7.27	0.56	6.27	4.36	8.19	0.98	10.21	5.57	14.85	2.37	35.13	30.88	39.38	2.17
29	6.18	5.06	7.31	0.57	6.33	4.37	8.28	1	10.37	5.62	15.11	2.42	35.5	31.26	39.74	2.16
30	6.19	5.04	7.34	0.59	6.38	4.38	8.37	1.02	10.52	5.66	15.37	2.48	35.81	31.57	40.05	2.16
31	6.2	5.03	7.37	0.6	6.42	4.38	8.46	1.04	10.67	5.7	15.63	2.53	36.14	31.9	40.37	2.16
32	6.21	5.01	7.4	0.61	6.47	4.38	8.55	1.06	10.81	5.73	15.89	2.59	36.45	32.21	40.68	2.16
33	6.21	4.99	7.43	0.62	6.51	4.37	8.64	1.09	10.95	5.75	16.16	2.65	36.75	32.51	40.99	2.16
34	6.22	4.98	7.45	0.63	6.54	4.36	8.72	1.11	11.09	5.77	16.41	2.72	37.04	32.8	41.28	2.16
35	6.22	4.97	7.47	0.64	6.58	4.35	8.8	1.13	11.23	5.78	16.67	2.78	37.32	33.07	41.57	2.17
36	6.22	4.95	7.49	0.65	6.61	4.34	8.87	1.16	11.36	5.78	16.93	2.84	37.59	33.33	41.84	2.17
37	6.23	4.94	7.51	0.65	6.63	4.32	8.95	1.18	11.49	5.78	17.19	2.91	37.84	33.58	42.11	2.18
38	6.23	4.93	7.52	0.66	6.66	4.3	9.02	1.2	11.61	5.78	17.45	2.98	38.09	33.81	42.37	2.18
39	6.23	4.92	7.53	0.67	6.68	4.29	9.08	1.22	11.73	5.76	17.7	3.05	38.33	34.04	42.63	2.19
40	6.23	4.92	7.54	0.67	6.71	4.27	9.14	1.24	11.85	5.75	17.96	3.12	38.56	34.25	42.87	2.2
41	6.23	4.91	7.55	0.67	6.73	4.25	9.2	1.26	11.97	5.72	18.21	3.19	38.79	34.45	43.12	2.21
42	6.23	4.9	7.56	0.68	6.74	4.23	9.26	1.28	12.08	5.7	18.47	3.26	39	34.65	43.35	2.22
43	6.23	4.9	7.57	0.68	6.76	4.21	9.32	1.3	12.19	5.67	18.72	3.33	39.21	34.83	43.58	2.23
44	6.23	4.89	7.57	0.68	6.78	4.19	9.37	1.32	12.3	5.63	18.97	3.4	39.41	35	43.81	2.25
45	6.24	4.89	7.58	0.69	6.79	4.17	9.42	1.34	12.41	5.59	19.23	3.48	39.6	35.16	44.03	2.26
46	6.24	4.89	7.58	0.69	6.81	4.15	9.46	1.36	12.51	5.54	19.48	3.55	39.78	35.31	44.25	2.28
47	6.24	4.88	7.59	0.69	6.82	4.13	9.5	1.37	12.61	5.49	19.72	3.63	39.96	35.45	44.46	2.3
48	6.24	4.88	7.59	0.69	6.83	4.11	9.55	1.39	12.71	5.44	19.97	3.71	40.13	35.59	44.67	2.32
49	6.24	4.88	7.59	0.69	6.84	4.09	9.58	1.4	12.8	5.39	20.22	3.78	40.3	35.71	44.88	2.34
50	6.24	4.88	7.6	0.69	6.85	4.08	9.62	1.41	12.9	5.33	20.46	3.86	40.46	35.83	45.08	2.36
51	6.24	4.88	7.6	0.69	6.86	4.06	9.65	1.43	12.99	5.27	20.71	3.94	40.61	35.93	45.28	2.39
52	6.24	4.87	7.6	0.7	6.87	4.04	9.69	1.44	13.08	5.2	20.95	4.02	40.76	36.03	45.48	2.41

(A.1 continued)

S	Foredune				Slack				Backdune				Bush			
	S_{est}	LB	UB	SD	S_{est}	LB	UB	SD	S_{est}	LB	UB	SD	S_{est}	LB	UB	SD
53	6.24	4.87	7.6	0.7	6.87	4.03	9.72	1.45	13.16	5.13	21.19	4.1	40.9	36.12	45.67	2.44
54	6.24	4.87	7.6	0.7	6.88	4.01	9.75	1.46	13.25	5.06	21.43	4.18	41.04	36.21	45.86	2.46
55	6.24	4.87	7.6	0.7	6.89	4	9.77	1.47	13.33	4.99	21.67	4.25	41.17	36.28	46.05	2.49
56	6.24	4.87	7.61	0.7	6.89	3.99	9.8	1.48	13.41	4.91	21.9	4.33	41.29	36.35	46.24	2.52
57	6.24	4.87	7.61	0.7	6.9	3.97	9.82	1.49	13.49	4.84	22.14	4.41	41.42	36.41	46.42	2.55
58	6.24	4.87	7.61	0.7	6.9	3.96	9.84	1.5	13.56	4.76	22.37	4.49	41.54	36.47	46.6	2.58
59	6.24	4.87	7.61	0.7	6.91	3.95	9.86	1.51	13.64	4.68	22.6	4.57	41.65	36.52	46.78	2.62
60	6.24	4.87	7.61	0.7	6.91	3.94	9.88	1.52	13.71	4.59	22.83	4.65	41.76	36.57	46.95	2.65
61	6.24	4.87	7.61	0.7	6.91	3.93	9.9	1.52	13.78	4.51	23.05	4.73	41.86	36.61	47.12	2.68
62	6.24	4.87	7.61	0.7	6.92	3.92	9.92	1.53	13.85	4.42	23.28	4.81	41.97	36.64	47.29	2.72
63	6.24	4.87	7.61	0.7	6.92	3.91	9.94	1.54	13.92	4.33	23.5	4.89	42.06	36.67	47.46	2.75

APPENDIX B. SUPPLEMENTARY MATERIAL FOR CHAPTER 3

B.1 Results of Permutational ANOVA (PERMANOVA) applied on coastal dune ants in five locations (Saint Joseph Peninsula Preserve State Park, Saint Andrews State Park, Grayton Beach State Park, Topsail Hill Preserve State Park, and Bon Secour National Wildlife Refuge). Habitat is the fixed factor and the location is random factor. Significant results ($P \leqslant 0.05$) are bold.

Source	df	SS	MS	Pseudo-F	P(perm)	perms	P(MC)
Habitat	3	14.877	4.9589	9.1046	0.0002	9941	0.0006
Location	4	1.5902	0.39755	3.3394	0.0019	9942	0.0018
Habitat x location	12	6.6235	0.55196	4.6364	0.0001	9919	0.0001
Res	119	14.167	0.11905				
Total	138	37.644					

B.2 Results of Pair-wise tests comparing ant communities of same habitat in different locations. SJ: Saint Joseph Peninsula Preserve State Park; SA: Saint Andrews State Park; GB: Grayton Beach State Park; TH: Topsail Hill Preserve State Park; BS: and Bon Secour National Wildlife Refuge. Significant results ($P < 0.05$) are bold. Note that the following tables are the data for foredune, slack, backdune, and bush, respectively.

B.2.1 Within level 'foredune' of factor 'Habitat'

Groups	t	P(perm)	Unique perms	P(MC)
SJ, SA	2.9388	0.0512	232	0.0572
SJ, GB	3.3289	0.0406	119	0.0365
SJ, TH	2.0946	0.0968	136	0.1091
SJ, BS	4.6665	0.0003	253	0.0037
SA, GB	0.72103	0.6021	33	0.5793
SA, TH	0.56247	0.6114	102	0.502
SA, BS	3.3955	0.0025	75	0.006
GB, TH	1.2974	0.3082	31	0.2762
GB, BS	3.4043	0.0034	38	0.0036
TH, BS	2.117	0.0021	65	0.102

B.2.2 Within level 'slack' of factor 'Habitat'

Groups	t	P(perm)	Unique perms	P(MC)
SJ, SA	1.4596	0.179	65	0.2059
SJ, GB	Negative			
SJ, TH	1.5937	0.1558	345	0.1513
SJ, BS	3.167	0.0301	12	0.0167
SA, GB	0.91963	0.4704	248	0.4035
SA, TH	1.9123	0.0821	495	0.0928
SA, BS	6.5631	0.0002	71	0.0002

(B.2.2 continued)

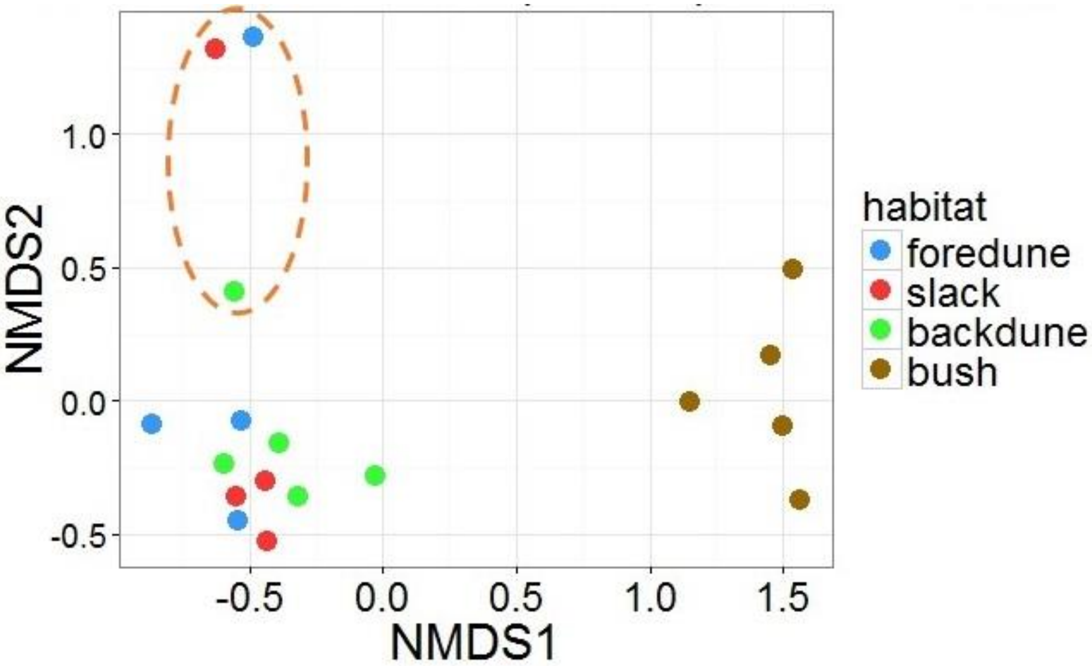
Groups	t	P(perm)	Unique perms	P(MC)
GB, TH	2.1618	0.0524	1771	0.0724
GB, BS	6.317	0.0019	54	0.0064
TH, BS	3.152	0.0011	96	0.0098

B.2.3 Within level 'backdune' of factor 'Habitat'

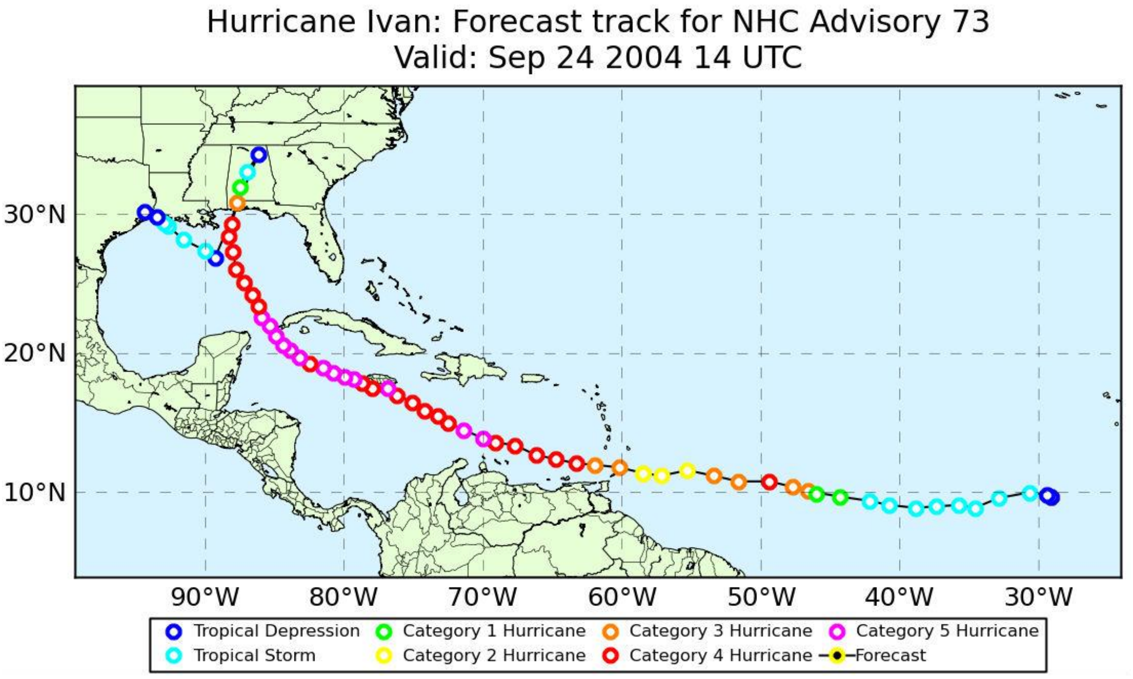
Groups	t	P(perm)	Unique perms	P(MC)
SJ, SA	1.5491	0.1743	539	0.1739
SJ, GB	1.1593	0.2746	177	0.2828
SJ, TH	2.0317	0.0235	474	0.0387
SJ, BS	2.2829	0.0337	273	0.0383
SA, GB	Negative			
SA, TH	0.61724	0.6288	2168	0.6265
SA, BS	Negative			
GB, TH	1.3222	0.2427	1038	0.2352
GB, BS	1.1781	0.2456	246	0.3001
TH, BS	1.7686	0.0663	812	0.0825

B.2.4 Within level 'bush' of factor 'Habitat'

Groups	t	P(perm)	Unique perms	P(MC)
SJ, SA	2.0004	0.0443	2892	0.0794
SJ, GB	2.5309	0.0133	1287	0.0452
SJ, TH	2.2678	0.0195	5089	0.0613
SJ, BS	3.0831	0.0071	5074	0.0384
SA, GB	0.46859	0.709	462	0.6861
SA, TH	1.5614	0.1861	2901	0.1896
SA, BS	2.8004	0.0049	1712	0.016
GB, TH	1.8249	0.1522	1287	0.1441
GB, BS	4.6522	0.0026	792	0.0052
TH, BS	1.5586	0.2651	5053	0.2247



B.3 Non-metric multidimensional scaling (based on Jaccard similarity index) for ant species composition of coastal dunes in five locations. Three dots in the dash ellipse represent ant communities in Bon Secour National Wildlife Refuge.



B.4 Map showing the track and intensity of Hurricane Ivan. Recourse: LSU Earth Scan Laboratory (https://www.esl.lsu.edu/hurricanes/2004/IVAN/)

APPENDIX C. SUPPLEMENTARY MATERIAL FOR CHAPTER 7

C.1 Confidence Intervals (CI) and Standard Deviation (SD) of sample based rarefaction and extrapolation curves of cypress, tupelo, and maple based on an average of series of 1,000 randomizations of the data. S_{est}: estimated number of species; LB: 95% CI Lower Bound; UB: 95% CI Upper Bound.

Sample	whole tree				canopy				trunk			
	S_{est}	LB	UB	SD	S_{est}	LB	UB	SD	S_{est}	LB	UB	SD
1	5.59	3.37	7.8	1.13	3.34	1.64	5.04	0.87	4.63	2.7	6.57	0.99
2	8.46	5.64	11.28	1.44	5.28	3	7.56	1.17	7.35	4.73	9.97	1.34
3	10.27	7.25	13.28	1.54	6.59	4.1	9.08	1.27	9.17	6.28	12.06	1.48
4	11.54	8.48	14.61	1.57	7.58	5.03	10.13	1.3	10.51	7.49	13.53	1.54
5	12.52	9.45	15.59	1.57	8.37	5.82	10.92	1.3	11.55	8.47	14.63	1.57
6	13.29	10.25	16.33	1.55	9.03	6.51	11.56	1.29	12.4	9.3	15.5	1.58
7	13.93	10.93	16.92	1.53	9.61	7.12	12.1	1.27	13.1	10	16.2	1.58
8	14.47	11.53	17.4	1.5	10.11	7.67	12.55	1.25	13.7	10.62	16.78	1.57
9	14.93	12.05	17.8	1.46	10.56	8.17	12.95	1.22	14.21	11.16	17.26	1.55
10	15.33	12.53	18.13	1.43	10.96	8.62	13.3	1.19	14.66	11.65	17.66	1.53
11	15.68	12.96	18.4	1.39	11.32	9.03	13.61	1.17	15.05	12.09	18.01	1.51
12	16	13.35	18.64	1.35	11.65	9.42	13.89	1.14	15.4	12.49	18.31	1.48
13	16.29	13.72	18.85	1.31	11.95	9.77	14.14	1.11	15.72	12.87	18.58	1.46
14	16.55	14.06	19.03	1.27	12.23	10.09	14.37	1.09	16.01	13.21	18.81	1.43
15	16.79	14.38	19.2	1.23	12.49	10.4	14.58	1.07	16.28	13.53	19.02	1.4
16	17.01	14.68	19.34	1.19	12.72	10.68	14.77	1.04	16.52	13.83	19.21	1.37
17	17.22	14.97	19.48	1.15	12.94	10.94	14.95	1.02	16.75	14.12	19.38	1.34
18	17.42	15.24	19.6	1.11	13.15	11.18	15.11	1	16.96	14.38	19.54	1.32
19	17.61	15.5	19.71	1.07	13.33	11.41	15.26	0.98	17.16	14.64	19.69	1.29
20	17.78	15.75	19.81	1.04	13.51	11.62	15.4	0.97	17.35	14.88	19.83	1.26
21	17.95	15.99	19.91	1	13.67	11.81	15.53	0.95	17.53	15.11	19.96	1.24
22	18.11	16.21	20	0.97	13.83	12	15.65	0.93	17.7	15.33	20.08	1.21
23	18.26	16.43	20.09	0.93	13.97	12.17	15.77	0.92	17.86	15.53	20.19	1.19
24	18.4	16.64	20.17	0.9	14.1	12.34	15.87	0.9	18.02	15.73	20.3	1.17

(C.1 continued)

Sample	whole tree				canopy				trunk			
	S_{est}	LB	UB	SD	S_{est}	LB	UB	SD	S_{est}	LB	UB	SD
25	18.54	16.84	20.25	0.87	14.23	12.49	15.97	0.89	18.17	15.92	20.41	1.14
26	18.68	17.03	20.32	0.84	14.35	12.63	16.06	0.88	18.31	16.11	20.5	1.12
27	18.8	17.21	20.39	0.81	14.46	12.76	16.15	0.86	18.44	16.28	20.6	1.1
28	18.92	17.39	20.46	0.78	14.56	12.89	16.23	0.85	18.57	16.45	20.69	1.08
29	19.04	17.56	20.52	0.75	14.66	13.01	16.3	0.84	18.69	16.61	20.78	1.06
30	19.15	17.73	20.58	0.73	14.75	13.12	16.37	0.83	18.81	16.77	20.86	1.04
31	19.26	17.88	20.64	0.7	14.83	13.22	16.44	0.82	18.93	16.92	20.94	1.03
32	19.36	18.03	20.7	0.68	14.91	13.32	16.5	0.81	19.04	17.06	21.02	1.01
33	19.46	18.18	20.75	0.66	14.99	13.41	16.56	0.8	19.14	17.2	21.09	0.99
34	19.56	18.32	20.8	0.63	15.06	13.5	16.61	0.79	19.25	17.33	21.17	0.98
35	19.65	18.45	20.85	0.61	15.12	13.58	16.66	0.79	19.35	17.45	21.24	0.96
36	19.74	18.58	20.9	0.59	15.19	13.66	16.71	0.78	19.44	17.58	21.3	0.95
37	19.82	18.7	20.95	0.57	15.25	13.73	16.76	0.77	19.53	17.69	21.37	0.94
38	19.9	18.81	20.99	0.56	15.3	13.8	16.8	0.76	19.62	17.8	21.43	0.93
39	19.98	18.92	21.03	0.54	15.35	13.87	16.84	0.76	19.7	17.91	21.5	0.91
40	20.05	19.03	21.07	0.52	15.4	13.93	16.87	0.75	19.79	18.02	21.56	0.9
41	20.12	19.13	21.11	0.51	15.45	13.99	16.91	0.75	19.86	18.11	21.61	0.89
42	20.19	19.23	21.15	0.49	15.49	14.04	16.94	0.74	19.94	18.21	21.67	0.88
43	20.25	19.32	21.19	0.48	15.53	14.09	16.97	0.73	20.01	18.3	21.72	0.87
44	20.32	19.41	21.22	0.46	15.57	14.14	17	0.73	20.08	18.39	21.78	0.86
45	20.37	19.49	21.26	0.45	15.6	14.18	17.03	0.72	20.15	18.47	21.83	0.86
46	20.43	19.57	21.29	0.44	15.64	14.23	17.05	0.72	20.22	18.55	21.88	0.85
47	20.48	19.64	21.32	0.43	15.67	14.27	17.07	0.72	20.28	18.63	21.93	0.84
48	20.53	19.71	21.35	0.42	15.7	14.31	17.1	0.71	20.34	18.7	21.98	0.84
49	20.58	19.78	21.38	0.41	15.73	14.34	17.12	0.71	20.4	18.77	22.02	0.83
50	20.63	19.84	21.41	0.4	15.76	14.37	17.14	0.71	20.46	18.84	22.07	0.82
51	20.67	19.9	21.44	0.39	15.78	14.41	17.16	0.7	20.51	18.9	22.11	0.82
52	20.71	19.95	21.46	0.39	15.81	14.44	17.18	0.7	20.56	18.96	22.15	0.81

(C.1 continued)

Sample	whole tree				canopy				trunk			
	S_{est}	LB	UB	SD	S_{est}	LB	UB	SD	S_{est}	LB	UB	SD
53	20.75	20	21.49	0.38	15.83	14.46	17.2	0.7	20.61	19.02	22.2	0.81
54	20.78	20.05	21.51	0.37	15.85	14.49	17.22	0.7	20.65	19.07	22.24	0.81
55	20.81	20.09	21.54	0.37	15.87	14.51	17.23	0.69	20.7	19.12	22.28	0.8
56	20.84	20.13	21.56	0.36	15.89	14.54	17.25	0.69	20.74	19.17	22.32	0.8
57	20.87	20.17	21.58	0.36	15.91	14.56	17.27	0.69	20.79	19.22	22.35	0.8
58	20.9	20.2	21.6	0.36	15.93	14.58	17.29	0.69	20.83	19.26	22.39	0.8
59	20.92	20.23	21.62	0.35	15.95	14.6	17.3	0.69	20.86	19.3	22.43	0.8
60	20.95	20.26	21.64	0.35	15.97	14.61	17.32	0.69	20.9	19.34	22.46	0.8
61	20.97	20.28	21.65	0.35	15.98	14.63	17.34	0.69	20.93	19.37	22.5	0.8
62	20.98	20.3	21.67	0.35	16	14.65	17.35	0.69	20.97	19.41	22.53	0.8
63	21	20.31	21.69	0.35					21	19.44	22.56	0.8

C.2 Confidence Intervals (CI) and Standard Deviation (SD) of sample based rarefaction curves of whole tree, canopy, and trunk based on an average of series of 1,000 randomizations of the data. S_{est}: estimated number of species; LB: 95% CI Lower Bound; UB: 95% CI Upper Bound.

Sample	cypress				tupelo				maple			
	S_{est}	LB	UB	SD	S_{est}	LB	UB	SD	S_{est}	LB	UB	SD
1	5.5	3.43	7.58	1.06	5.43	3.41	7.45	1.03	5.94	3.21	8.68	1.4
2	8.32	5.71	10.92	1.33	8.18	5.82	10.55	1.21	8.69	5.36	12.02	1.7
3	10.03	7.31	12.74	1.39	9.95	7.5	12.41	1.25	10.47	6.93	14	1.8
4	11.21	8.52	13.91	1.38	11.19	8.73	13.64	1.25	11.72	8.09	15.36	1.86
5	12.1	9.47	14.74	1.34	12.09	9.66	14.52	1.24	12.78	9.09	16.46	1.88
6	12.81	10.25	15.36	1.3	12.78	10.39	15.16	1.22	13.67	9.96	17.38	1.89
7	13.38	10.91	15.86	1.26	13.31	10.97	15.65	1.19	14.45	10.72	18.17	1.9
8	13.87	11.47	16.26	1.22	13.74	11.44	16.03	1.17	15.14	11.4	18.88	1.91
9	14.28	11.96	16.6	1.18	14.08	11.83	16.33	1.15	15.76	12	19.52	1.92
10	14.65	12.4	16.9	1.15	14.37	12.17	16.56	1.12	16.33	12.55	20.11	1.93
11	14.97	12.78	17.15	1.11	14.59	12.44	16.74	1.1	16.85	13.04	20.67	1.94
12	15.23	13.1	17.36	1.09	14.79	12.68	16.89	1.07	17.34	13.5	21.19	1.96
13	15.48	13.39	17.56	1.06	14.95	12.89	17.02	1.05	17.8	13.91	21.69	1.99
14	15.69	13.66	17.73	1.04	15.1	13.08	17.12	1.03	18.23	14.28	22.17	2.01
15	15.89	13.89	17.89	1.02	15.23	13.25	17.21	1.01	18.63	14.61	22.64	2.05
16	16.07	14.1	18.03	1	15.35	13.4	17.3	0.99	19	14.92	23.08	2.08
17	16.23	14.29	18.16	0.99	15.45	13.53	17.37	0.98	19.35	15.18	23.52	2.13
18	16.37	14.46	18.28	0.97	15.55	13.66	17.45	0.97	19.68	15.42	23.94	2.17
19	16.5	14.61	18.39	0.96	15.65	13.77	17.52	0.96	19.99	15.62	24.36	2.23
20	16.62	14.74	18.49	0.96	15.74	13.88	17.6	0.95	20.28	15.8	24.76	2.29
21	16.73	14.86	18.59	0.95	15.83	13.97	17.68	0.95	20.55	15.94	25.16	2.35
22	16.83	14.97	18.69	0.95	15.91	14.06	17.77	0.95	20.81	16.06	25.56	2.42
23	16.92	15.06	18.78	0.95	16	14.14	17.86	0.95	21.04	16.15	25.94	2.5
24	17	15.13	18.87	0.95	16.08	14.2	17.96	0.96	21.27	16.22	26.32	2.58

APPENDIX D. LETTER OF PERMISSION

Letter of permission from *Journal of Insect Conversation*

Title: Ant community structure and response to disturbances on coastal dunes of Gulf of Mexico

Author: Xuan Chen

Publication: Journal of Insect Conservation

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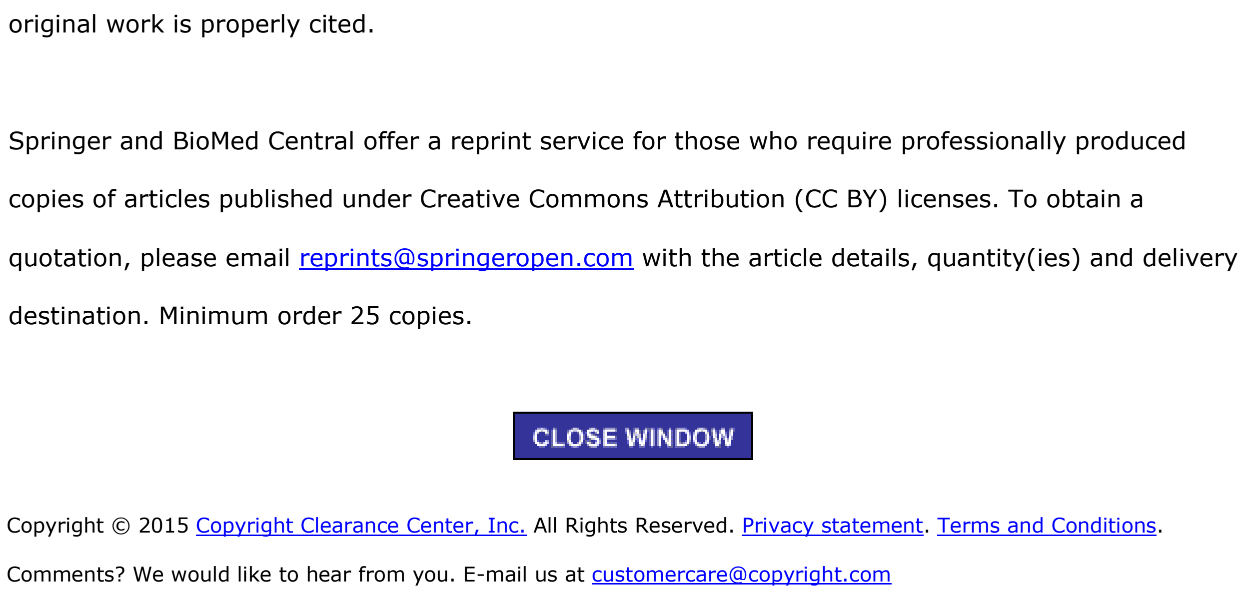

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VITA

Xuan Chen was born in Hulin of Heilongjiang Province of China. The family later moved to Beijing where he received a bachelor degree at the China Agriculture University (CAU) in 2006. In the same year, he enrolled in the Department of Entomology of CAU and received the Masters degree in 2009. Then he received a scholarship from Louisiana State University in 2009 to become a Graduate Assistant in the same year.