LIVING ON THE EDGE: ANTS ON THE DUNES OF GEORGIA’S BARRIER ISLANDS

by

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(Under the Direction of Brian T. Forschler)

ABSTRACT

Bait surveys were undertaken in the summers of 2016 and 2017 for ants on the primary dunes of three Georgian barrier islands. Species diversity was higher than expected, with multiple new records for the state. Assemblage abundance and incidence data indicate each island to be at a different stage of invasion by *Solenopsis invicta*, the red imported fire ant, with the ant assemblage composition and species richness of each islands affected by the degree of *S. invicta* presence. Collaborating sea turtle monitoring programs throughout the state collected ants from sea turtle nests which were most commonly *S. invicta*, but also multiple native ant species, implying that sea turtle nests may be an opportunistically scavenged resource by both invasive and native ants.

INDEX WORDS: Ant assemblage, Ant diversity, Caretta caretta, Formicidae, Island biogeography, Loggerhead sea turtle, Primary dune, Red Imported Fire Ant, Solenopsis invicta,

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DEDICATION

For ants and turtles and everyone who loves exploring

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CHAPTER 1

The State of Research on the Insects of Coastal Dunes and Sandy Beaches: Georgia's Barrier Islands as a Model Ecosystem

Insects associated with sandy dunes and beaches are an understudied group of organisms. This paper serves to explore some of the historical reasons for that initial lack of attention and review the concepts and ecological roles we have more recently begun to understand. To name just a few: insects in coastal areas function as a link between marine and terrestrial food webs, they can serve as bioindicators of ecosystem health, but they can also become invaders altering community compositions and endangering at risk populations. The challenge in understanding these types of dynamics and functions is that without an initial baseline for understanding a coastal community, it becomes difficult to understand or predict future trends for dynamic coastal ecosystems.

This work attempts to bring together the current research from across a broad range of life science disciplines to create a context for understanding the "why" behind some of the historical challenges to this kind of research while forming a framework of our current understanding of insects in sandy beach-dune ecosystems.

Sandy shore research

The beach, the portion of the coastline that comes into contact with ocean waves and spray, has at its inland edge a foredune of mounded sand where vegetation can establish. The two are ecologically linked, however research in coastal habitats often focuses on one are or the other.

The ecology of sandy shores is an emerging area of ecological research. Nel et al (2014) note sandy beaches were not recognized as an independently functioning ecosystem until the 1980's with the majority of sandy beach literature comes from just four areas, the United States, Brazil/Uruguay, South Africa, and the Mediterranean around Italy [120]. From work in those areas, models have been developed that characterize arthropod distribution along a gradient of shore zones, which are often tightly bounded and controlled by vegetation and microclimate conditions.

The literature investigating insects in coastal dunes is scarce. A possible reason for this was an initial misunderstanding of the actual presence of insects in beach-dune habitats. Research studying macroarthropods on beaches tends to focus on crustaceans, especially copepods and amphipods, often without insects even being considered (e.g. [20]). Deidun and Schembri [52] point out that as recently as 1990 a beach ecology textbook [22] taught that insects as a clade had failed to establish on beaches, with the habitat being essentially marine. This traditional thinking that insects do not function in coastal marine environments could lead to them being discarded or overlooked in coastal studies. Even as researchers have become more aware of insects as a contributing factor in coastal ecosystems, previous misconceptions make analysis difficult. Defeo et al.'s (2017) metanalysis on patterns of macrofaunal diversity of the world's sandy beaches completely excluded insects and arachnids from their dataset, noting that terrestrial arthropods are rarely considered in beach surveys and even when insect were intentionally collected the standard methods for beach sampling work poorly for collecting highly mobile or flying organisms [50]. These institutional oversites appear to be related in large part to crustaceans often being study organisms of interest and the resulting sampling methods.

The standard collecting methods for studies of beach arthropods are vulnerable to excluding insects from beach surveys. A beach-dune system consists of a series of zones defined by changes in water availability, tide swash, and establishment of vegetation to establish. The eulittoral zone of the beach consistently becomes inundated by tides and has little to no vegetation. The supralittoral zone has ocean spray, accumulation of debris washed up by hightide as wrack, and while occasionally inundated during storms or other exceptional high tides tends to remain above water allowing hardy pioneer plants to establish. These plants anchor and accumulate sand, forming a primary dune over time which functions as a barrier from further encroachment of tides and ocean spray barring all but the most extreme conditions, creating an extralittoral zone with several dunes further inland of the primary dune. An excellent diagram of these zones can be seen in Figure 1 from Fallaci, Colombini, and Chelazzi (1994) [63]. Much of the sampling for sandy beach macrofauna focuses exclusively on the eulittoral or intertidal zone, shown in more detail in Figure 2, a diagram of the intertidal zone from Dugan et al. 2013 [58]. When sampling for macroarthropods, studies often use of combination of pitfalls, hand collecting, and sediment cores from the base of the primary (first) dune through the eulittoral zone (e.g. [16, 72]). Even as recently as 2017, papers about the questions of concern on beaches often focus on the intertidal zone, but Jones et al. 2017 at least acknowledges that “intertidal beaches have close ecological linkages with contiguous subtidal and dune ecosystems.” [91]. Older beach diversity studies use solely core

Figure 1:Diagram of the intertidal zone from Dugan et al. 2013

sampling (e.g. [57]) which is efficient for collecting sand dwelling isopods and amphipods, but the assumption of the method is that those are the only arthropod organisms that live on beaches. A few papers like Barboza et al.'s (2012) include pitfalls and acknowledge that their sampling methods underestimate insect richness and abundance [16], but this is a recent phenomenon.

While there have been unintentional limitations to studying beach-dune dwelling insect arthropods, two main groups have increased our knowledge of those assemblages. One is a working group out of Italy led by Colombini, Chelazzi, and Fallaci [29, 32-41, 63-65, 69]. They seem, as others, to have an inordinate fondness for beetles, and over several decades have done a series of experiments and observations looking at the distribution and community assemblage and beach-dune systems, with a special focus on Tenebrionidae.

Fallaci et al. (1997) examined niche partitioning of tenebrionid beetles [64]. Previous work had shown night-active darkling beetles stayed in the eu- and supralittoral zones, but the 4 crepuscular species they followed inhabited vegetated dune habitats with forays onto the beach. The night active beetles appear to never venture onto the dunes, however. They also noted that differences in measured abundance of species collected was in part due to differences in the mobility of the species, with less mobile species being collected less frequently but not necessarily having smaller populations. The beetles also partitioned their activity to different time portions of the day based on their relative degree of thermophily, allowing multiple sympatric species to occupy the same space via temporal resource partitioning. The authors noted this behavior to be consistent with literature on species in other arid and semi-arid habitats, where daily activity rhythms correspond to ambient daily temperatures to create a variable daily activity pattern of species within the community. They also noted that species with a high degree of plasticity have an advantage in survival on coastal sand dunes due to the variability of environmental conditions in the dune habitat. Thus some beach-dune insects undergo both spatial and temporal niche partitioning to allow multiple species to inhabit the same environment. While shown in studies on beetles, it seems quite possible that other terrestrial insects, like ants, exhibit similar behavior in these habitats.

Chelazzi et al.'s (2005) survey of beach and dune Coleoptera in Apulia used pitfalls and soil sieving [29]. Using data from the nearest climate station and microclimate data at each pitfall trap during sampling, they found a trend of zone preference by species, with some beetles more common in the eulittoral zone, others the dunes, and a group in an intermediate zone with each group's distribution varying by season. They collected 48 species, with greater abundance and species richness on the beach which they took as evidence to conclude that the beach was in "moderately good health" [29].

Colombini et al.'s (2005a) follow up work in Morocco studied isopods and coleopterans, using pitfall pentagonal traps sampling the eulittoral, supralittoral, and dune as well as placing cages around vegetation to evaluate the macrofaunal to plant biomass ratio [34]. By 2005 the group saw Coleoptera as most representative of the beach-dune system. However, they reported other organisms in capturing over 50,000 arthropods, with Isopods, Collembolan, Hymenoptera, Amphipoda, and Coleoptera being abundant in that order during the spring. There was a seasonal shift, however, with collembola overwhelmingly abundant (72.35%) compared to Coleoptera (0.84%) in the autumn.

Hymenoptera were concentrated on the dune and tied to the dune vegetation, but also were the most abundant beach insect group in the spring, although ants were only identified to Formicidae. The dominance of Collembola appears to be a common feature of both Mediterranean beaches and arid coastal areas in general, but would not be expected in a more humid climate like Georgia's.

Another area where beach insects have been studied along with marine arthropods to examine trends of environmental conditions related to animal distribution and abundance is a body of work coming out of Uruguay and Brazil. The main themes of their work are illustrated in Figure 3, taken from Barboza et al. (2012). Defeo and McLachlan (2011) [48] set out initially to link the morphological traits of sandy beaches to the community composition of beach dwelling macrofauna, splitting macrofauna into four groups: molluscs, polycheates, crustaceans, and insects. Their metanalysis of 63 sandy beach surveys documented species richness along with physical beach descriptions, paying attention to both supralittoral (air breathing) as well as intertertidal (water breathing) organisms. Their modeling showed that wave energy, tidal range, and beach particle size all had an effect on species richness, most easily parsed (they argue) by considering beach face slope which can be an easily measured proxy for all three. Their work showed that insects follow the same trends as the other three organismal groups, with species richness increasing on beaches with flatter slopes and finer sands, with crustaceans having a higher tolerance for courser sands and some variation in trends depending on if the crustaceans were intertidal or supralittoral species. Density of organisms collected also increased as beach slope decreased. While the paper is mostly focused on the physical parameters of beaches and how they correlate to marine organism communities, they point out that supralittoral insect communities responded in the opposite manner from crustaceans but followed the trends of intertidal organism, indicating a missing part of the knowledge of beach communities when dunes are not sampled. Crustaceans were also the only organisms which had representatives in both intertidal and supralittoral areas. It appears that perhaps one of the reasons insects have been historically overlooked on beaches is that for researchers coming from a marine perspective, sampling in the intertidal and swash zones collected all of the taxa of interest to their fields, a possibility Defeo and McLachlan seem to confirm with their comment of the need to study the dunes as well.

Defeo and McLachlan (2013) [49], working with a global data set of intertidal arthropods on 201 sandy beaches continued to develop their model of underlying trends relating arthropod diversity and abundance to beach morphological traits. As one would expect, species richness increased from temperate to tropical beaches. However, abundance seems tied to both latitude and beach slope, with higher species abundance in gentle sloped beaches in temperate areas. Dissipative beaches; beaches where sand is usually a fine particle size and the beach is broad and gently sloped with many sand bars to dissipate incoming wave energy [110], tend to have higher arthropod species richness, abundance, and biomass than their reflective beach counterparts. More recent work has shown that dissipative sandy beaches in South America also tend to have higher primary productivity, which can also increase faunal diversity and abundance [50]. One of Defeo and McLachlan’s additional insights was that “dissipative beaches harbor communities with highest abundance and species with the smallest body sizes.” The authors point out that one area particularly lacking in these types of data is beaches in the northern hemisphere. While the authors threw out data on insects and focused solely at organisms in the intertidal zone, their previous work showed insects follow similar trends to other beach arthropods. Considering the connectivity of the dunes/supratidal zone to the intertidal zone of coastal systems it stands to reason that some of the trends would hold for more interior habitats as well. Further, Georgia's beaches are in general gently sloped and dissipative, meaning one could expect to find a high diversity and abundance of arthropods there.

Mourglia, González-Vainer, and Defeo (2015) [119] noting the lack of research on insect fauna associated with beaches, except from the Mediterranean, conducted work on an Uruguayan beach. They expressly investigated the Littoral Active Zone (LAZ) which includes not just the beach intertidal zone but also the terrestrial dune system in a survey of the widest, most species rich beach in Uruguay [72].   Insect abundance and richness were highest in the summer, with the winter community being distinctly different from other seasons. The two most commonly occurring clades were formicids and tenebrionid beetles, with beetles being the main insect on the beach while ants were the main insects on the dunes, both in terms of species richness and abundance, regardless of season. The variation they observed in Formicidae species richness and abundance was best explained in their GLM by variation in sand moisture and elevation, with sand compaction also having a role in spatial variation. The two main ant species they collected were *Pheidole subarmata* Mayr, 1884, a common species that likes open soils and disturbed habitats, often found near sea shores [168], and *Dorymyrmex pyramicus* (Roger, 1863), a pyramid ant known to nest on littoral dunes. Ants in general preferred beach/dune areas characterized by high elevation, low soil moisture, and low sand compaction. Beetles preferred to forage in the beach zone near the shore line, especially in the summer but shifted closer to the base of the dunes in the winter. The richness and abundance of insects in the LAZ implies that insects have a more significant ecological role in the coastal ecosystem than researchers usually consider, with a need for further research into the biology and community of LAZ insects.

Barboza et al. (2012) working as part of Defeo's group out of Uruguay, investigated insects in their beach sampling along the estuaries of the Rio de la Plata [16]. Insects were 23% of the organisms they collected, and insect richness increased when beach conditions were dissipative. The authors took care to note that the insect richness was likely still underestimated because the sampling design only partially considered the dunes and also neglected night sampling when insects could be abundant. Insects were most predominantly present on high energy beaches with large swash zones where they forage on the upper swash areas. They also appeared to prefer beaches with higher sea surface salinity. These data led the authors to infer habitat and resource quality and availability were of importance to understanding insect communities in these habitats. Further, they noted the crucial need for considering life history when studying faunal biodiversity of any species group on sandy beaches.

Barboza and Defeo (2015) [17] explored the difference between reflective and dissipative beaches and the corresponding arthropod diversity trends, however they excluded terrestrial, landward distributed organisms, due to a lack of proper methodology in collecting them. Using a metanalysis of 256 sandy beaches from 5 continents, they were able to show that intertidal macrofaunal species richness was mainly predicted by grain size, beach slope, temperature, and tidal range on a global scale, suggesting that sandy beaches had predictable communities when their physical environment was considered. They noted that salinity and primary productivity did not have much explanatory power for species richness models, due to a lack of variation in salinity but without an explanation other than agreement with papers on other organismal systems for primary productivity. Perhaps the global scale is too broad when considering these factors.

Challenges to studying insects in coastal areas

One major challenge is understanding the life history, or at least feeding habits of insect organisms in these habitats. For example, Colombini et al. (2002) examined arthropods on a reflective Tunisian beach, from the shoreline to the dune base [32]. They reported two amphipods, an isopod, and five beetle species selected for analysis, noting that the distribution of carabids on the beach followed to an extent the distribution of washed up debris that the beetles are known to nest in (wrack). However, beetle resting sites appear to be distinct from foraging sites for the observed species. Further, highly mobile and/or predatory species seemed to be more uniformly distributed on the beach, while species preferring particular food sources or microclimate conditions were unevenly distributed. Thus the life history and feeding habits of insect organisms in these habitats is important to utilizing them as an indicator species, since a certain degree of specialization appears to occur. The need for better understanding the life history of beach insects so as to understand which research questions could be answered by collecting them was further emphasized in following work that noted the resting or active periods of tenebrionids [35].

Another challenge to studying insects in coastal areas comes from the assemblage variability by location. Colombini et al. (2003) noted the scarcity of information concerning terrestrial arthropods on beaches, especially a lack of studies that focused on more than one location [33]. They surveyed beaches throughout the Mediterranean basin in Malta, Morocco, Tunisia, and Italy from the high-water line to the backdune and found that beetle distribution shifted from the beach towards the dunes in the fall, and that tenebrionids, staphylinids, and anthicids were the most dominant groups. They also noted the trend of steeper beaches having more diverse beetle communities, which is contrary to the trends coming out of the research group from Uruguay (Figure 3), possibly due to the small beach width of Mediterranean shores making vegetation more common on more sloped beaches, resulting in increased plant richness in those locations and providing a richer habitat for beetles. High arthropod abundance numbers also appeared to correlate with low numbers of species for beetles. They emphasized the usefulness of beetle survey data such as theirs for assessing the health and monitoring impacts to beach ecosystems.

Studies focusing on the insect assemblage often find it to be species rich but dominated by a few highly abundant species [29]. One study of coastal dune beetles found a simple assembly of seven species dominated by just 2 that comprised 76% of abundance [66]. Similar trends of specious assemblages dominated by a few individuals also appear to be the norm for ants, as will be discussed later on. This trend makes it important to be aware of the need for the appropriate sampling effort, taking into account both rare species and microhabitats so that an accurate assessment is made of the assemblage.

Beach Wrack

Beach wrack, the most readily identifiable microhabitat on a beach, is defined as the vegetation and organic debris pushed on shore by waves to accumulate at the high tide line. Beach wrack has become an area of interest particularly for the potential that wrack can serve as a structural resource or provide insects that could be food for at-risk beach-nesting vertebrates as well as harbor bioindicator species (e.g. [71, 124, 133-135, 140]. There is a general succession, regulated by patch size, for beetles colonizing wrack with few species in bare sand near wrack [71]. The succession of beetles in wrack includes, by the second day, Staphilinids and Hydrophilids while Tenebrionids follow within three days with patch size affecting the number of colonizing species [71]. Fallaci et al. (2002) focused on the temporal and spatial difference between two widely distributed Tenebrionidae, *Phaleria provincialis* Fauvel, 1901 and *P. bimaculate* (L. 1767), at Burano Oasis and Parco Regionale della Maremma, Italy. Tenebrionids were sampled due to that family's conspicuous consumption of wrack on sandy beaches [65]. The authors point out that tenebrionids exist in higher species richness than the commonly studied talitrid and tylid crustaceans, making those beetle communities characteristic of the beaches they inhabit and a likely candidate as a bioindicator species [64].

The community of wrack colonizers also exhibit succession [37, 53]. Crustaceans and dipterans arrive immediately to within two days, followed by predatory staphylinids then tenebrionids a few days later. Crustaceans quickly abandon the wrack, and formicids and Aranei appear after a week as the wrack dries. One study recorded a higher proportion of female tenebrionids in the wrack compared to nearby pitfall traps, possibly indicating wrack as an egg harboring resource for some beetles [37] and first instar larvae arrived within a week, supporting this hypothesis. Isotope analysis showed that the fauna were not consuming the wrack, but it's physical structure provided a vital refuge resource from harsh environmental conditions and highlighted the importance of microclimate conditions for beach-dune dwelling organisms. Recent work out of Australia also investigated the colonization of beach wrack by invertebrates, where while a few percarid crustaceans dominated the abundance, being 71% of collected organisms, insects being 27% of the organisms collected were the majority (91%) of diversity with 62 out of the 68 species encountered [140]. The large and rapidly changing community of organisms that utilize wrack make it a highly visible microclimate with quite a few insect species utilizing the material over a short time in a healthy beach-dune system.

Wrack is one of the most directly observable links between the marine and terrestrial ecosystems. Wrack, and the organisms that thrive in it, provide not just habitat but also food web resources not just for insects but also to vertebrates like beach-nesting birds [140] or dune dwelling geckos[26] through wrack dwelling insects as a food source. High levels of wrack cover increase arthropod abundance, while wrack's mitigating effect on temperature, desiccation, and protection from UV most likely are the effects that bolstered insect diversity [140]. Wrack often begins the process of hummock and embryo dune formation by anchoring sand, eventually engendering the development of dune habitat, making it a physical as well as nutritional link between the marine and terrestrial systems [140].

Insects as Coastal Bioindicators

Through works such as the studies on wrack colonizers, a shift is starting to take place in how coastal researchers think about insects. Tenebrionids in particular have been proposed as very useful bioindicators because they are highly sensitive to habitat changes and could help predict effects of urbanization on beaches [74]. Further, insects perhaps are more influential than thought because the larger size, particularly of their larvae, allows them to contribute a large amount of biomass to food webs relative to more abundant yet smaller crustaceans [74]. Researchers like Colombini's works noting the higher site specificity of beetle assemblages at a beach-dune habitat due to increased insect species richness could be a useful tool both for evaluating newly studied systems and monitoring previously surveyed areas for changes. Focus on non-beetle insects is less developed and seems to have almost entirely come from dune studies. A few researchers, particularly in the Americas are starting to investigate ants.

Dunes and ants

Dunes in general can have a diverse insect assemblage. Howe et al.'s (2010) review of Welsh dunes reported 172 invertebrate species, (37% of the species collected) which depend on bare or sparsely vegetated sand habitats [85]. When they also added in species that specialize in bare sand micro-habitats of other dune zones, the total went up to 292 (63%) species collected. Hymenoptera in particular appear to be dependent on dunes due to their warmth-loving behavior and frequent dependence on pollen from long flowering plants. As a result, 278 such species can be found on Welsh sand dunes, 68% of the total aculeate Hymenoptera for the country. A similar survey of insects on a Scottish dune from 2011-2015 reported collecting 196 species, including 113 aculeate

Hymenoptera, almost half of the 243 known species in Scotland [128]. One would expect temperate and tropical areas, where more species in general occur, to also have high species richness on their dunes when sampled appropriately.

North American work has most recently studied dune insect assemblies. Timm and McGarigal's (2013) survey of Cape Cod's dune dwelling ground arthropods found Formicidae to be the most overwhelmingly abundant (76.1%) followed by Diptera (8.5%) and Araneae (5.5%) [153]. Their survey was focused on the potential prey items in the summer for dune dwelling vertebrates and found ants to be the main food source of a local amphibian, which is in turn the main prey item of a local snake, making ants a critical if not keystone component of the stuy's dune food web [153]. Timm and McGarigal further argue that the abundance and potential diversity of ants on dunes merits further research of these organisms [153]. Ellison's (2012) survey of Nantucket collected 58 of the 136 known (43%) known ant species in New England, higher than might be expected in such a developed, disturbed system, however maritime beach/dunes only had 13 of the study's collected species [62]. Mirroring the trend for many of the Mediterranean beetle studies [66], the Nantucket ant assemblage recovered eight commonly abundant species, with the others being rarely encountered.

The first study in Mexico to characterize coastal dune ants was published in 2014 [132]. Seven species made up 40.8% of total species occurrences, 2 *Solenopsis spp.*, *Dorymyrmex bicolor* Wheeler, 1906, and *Pheidole susannae* Forel, 1886 among them with 28 species only being encountered once. The study differentiated dunes by dominant vegetation, no difference was found in the number of species collected between the rainy and dry season and 121 species from 41 genera were collected overall. The bulk of species collected (69, 57%) were soil nesting species. Ants typical of disturbed environments were found in high abundance in every habitat. Only 4 species were found to nest in both the ground and vegetation, all of which were tramp or invasive species. The study indicates the tremendous possibility of ant species richness in dune habitats despite their often overlooked status is much of the historical coastal survey literature.

The extant surveys of coastal fauna, if they mention ants at all, often identify ants to the family level despite mentioning that they can be the most abundant organisms collected during the survey [37, 39, 41, 42, 80]. The rarity of papers discussing ants on beach-dune systems does not mean they are absent from the habitats, however. In addition to the previously mentioned work from Mexico, several other studies have found ants even in extreme marine environments. Morrison (2003) studied ants on small Bahamian cays of <1,000 m^2 vegetated area, and found that ants were almost always present on cays with vegetation, and never on cays without vegetation [114]. It is likely that ants, like beetles, are exploiting many microhabitats in these coastal areas. For instance, small colonies of fungus-growing basal Attini ants have been found on South American sandy beaches [94], preferring to build nests in the active dune zone with sparse vegetation [98] despite the lack of tremendous plant biomass needed by their more well known leaf cutter relatives. With these species, where colonies consist of fewer than 100 workers and a single entrance to the colony, it would be tremendously easy to miss the species in general surveys. *Mycetophylax simplex* (Emery, 1888) was only reported in Uruguay in 2016 as no previous study had looked at the ants on beaches [98], despite Uruguay being one of the main areas of sandy beach research. The authors point out that the presence of these species appears related to dune physical characteristics, distribution of resources, and availability of nesting places along with their association only with dune habitats make *M. simplex* and other dune ants quite useful as indicator species. Yensen et al. (1980) found *Brachymyrmex* and *Iridomyrmex* ant colonies in intertidal mud flats in Mexico that survived up to 149 inundations under sea water annually over a meter deep and lasting 3.5 hours [171]. Ants clearly can survive and thrive even in extreme coastal habitats, and it seems likely that areas where ants have not been reported in coastal arthropod surveys have merely not yet been sufficiently explored.

Chen et al. (2015) focused ant communities in disturbed and intact dunes along the Southeastern U.S. gulf coast [30]. 44 ant species were collected from the dunes, comprising all but one of Anderson's [7, 8] ant functional groups indicating dunes can have both species and functional richness. Ant diversity was lower in degraded and restoration sites, directly indicating ant species richness as a useful bioindicator tool for dune habitat health. Further, disturbance altered the composition of functional groups within ant assemblages, with changes in the dominant species (often *Forelius pruinosus* (Roger, 1863)) before and after restoration events and Dominant Invasive ants being present in degraded and restoration areas. Cryptic species were only found in the back dunes, indicating a need to study the full range of dune habitat to get the most accurate picture of the ant assemblage in these areas. Opportunists were the most diverse functional group recovered, due to their ability to adapt to the dynamic and challenging environment of the coastline. The vegetation structure on the dunes was found to significantly influence the ant community, with plant height, plant richness, and percent cover all related to higher levels of ant diversity. Chen et al. link this to the increased likelihood of microclimates in areas where these plant factors are high, in a parallel to the more robust work linking beach-dune beetle diversity to micro-habitats. Chen et al. also point out areas with these plant conditions may have higher arthropod diversity providing food and resources for more ants, indicating a less disturbed dune environment where plants and associated fauna to establish. No diversity trend was linked to leaf litter, but ant diversity was higher directly underneath bushes, again showcasing the importance of the association between plants and ants on dunes. *Dorymyrmex flavus* McCook 1880 and *F. pruinosus* were the most common ants in undisturbed dunes, while *Solenopsis invicta* Buren, 1972 was strongly associated with disturbed dune areas. Altogether, Chen et al. make a strong case for ants as valuable bioindicators for assessing dune health and environmental change over time.

Ants as invasive species

Ants are important to consider not just for their possible biodiversity, but also their potential as problematic invasive species. Invasive ants are understandably often focused on and have been researched and reviewed extensively (e.g. Bertelsmeier et al. 2016, Rabitsch 2011 [19, 129]). As such this review focuses on other aspects of the ecology and state of research on insects, but the topic still merits touching on. While recognized as an ongoing and large-scale issue, occurrences of invasive ants colonizing areas likely occurs more often than we even realize. Miravete et al. (2014) suggested that globally, the introduced ant species in temperate regions was up to three and a half times higher than the number of detected species, with 67% of those introduced species establishing in their new introduced habitats [112]. Further, they estimated roughly 13,000 ant species being transported by humans to new habitats, with the majority of species originating in the Neotropics. The mobility of ants could be of concern for areas like Georgia, which has two of that Atlantic coast's busiest ports in Brunswick and Savannah. Less developed and understudied coastlines could be at risk of undiscovered exotic ants due to their success as a globally mobile clade.

A few other reviews on ants worth considering are Rabitsch (2011) [129], which does a great job of laying out the life history traits that tend to make the invasion process successful although with a group as diverse as ants these traits vary. Russell et al. (2017) focused on invasive species on islands, particularly the traits and trends that make certain species successful invaders as well as their impacts on islands and biosecurity, management, or even eradication efforts [136].

The trends for invasive species can be complicated, however, when islands are involved. A studying comparing the assemblages of ant communities between inland, coastal, and island urban green areas found that a gradient existed of island > coastal > inland where islands are most vulnerable to invasion and inland areas were least vulnerable to invasion by exotic species [130]. Human visiting and inhabitation of islands, and the subsequent increase in disturbance events and transport of non-native species, appears to be having a dampening effect on traditional area and isolation island biogeography effects for ant communities [131], making it more challenging to predict the movement and likelihood of exotic ant invasion when islands have some degree of human activity.

Trends for ants on Islands

Islands arguably are the place where modern ecological thinking began. Eugene Odum's work in places like Sapelo Island (e.g. [139]), led to the publication of *Fundamentals of Ecology*, the first textbook for the field and helped shape the discipline of ecosystems based ecology. E.O. Wilson's work on Melanesian ants [166] led to work by MacArthur and Wilson [103] followed by Wilson and Simberloff's [142-145, 167] studies in the tropics and Florida keys. These works laid the foundation for Island Biogeography theory, shaping our modern understanding of community dynamics through species colonization, invasion, and extirpation. These concepts are still very much at the forefront of research attempting to understand the world around us [155]. Yet despite the massive amount of attention given to islands as nature's laboratories, the sandy shorelines and coastal dunes they contain have only recently begun to be scientifically explored.

Ants can serve as valuable island bioindicators [9, 10, 138] often having high species richness and functional diversity in healthy ecosystems. They are easy to collect under standardized protocols, and their large population sizes allow for organisms to be collected without stressing healthy communities [3]. Even without expert abilities to identify species, collected ants can be categorized into nine functional groups based on their basic behaviors and morphology of subfamilies to allow for the inference of localized community roles [7, 8]. More recently, the links between ant functional traits and environmental gradients have been studied [11-13], creating a possible framework for understanding research systems based on their localized ant fauna. One intriguing finding of this work is that ant functional diversity increases in open habitats [12], such as patchily vegetated beach dunes, meaning that areas like dunes which are often of conservation concern could be monitored by examining their ant fauna without placing undue stress on these notoriously fragile ecosystems. Despite coastal islands being an area of great interest for ecological modeling and research, it is rare to encounter work focusing on the sandy shore insect communities of these systems.

The documentation that does exist overwhelmingly focuses on invasive species colonizing or altering islands (e.g. [1, 24, 27, 45, 76, 79, 99, 100, 154, 156, 158, 161, 162, 164, 170]). This work is understandable, seeing as the Invasive Species Specialist Group lists five ant species among their list of the 100 worst invasive species [102]. Perhaps the area at the forefront of monitoring for and dealing with invasive species is Australia, where monitoring and proactive response have been effective at mitigating and in several cases (106 out of 316 attempts, but usually on areas smaller than 5 hectares [81, 82]) eradication of invasive ant species, even notorious ones like *Pheidole megacephala* (Fabricus, 1793), before they successfully establish. This monitoring has also accumulated a large amount of information about ant communities on islands, with recent work delineating cryptic island species, and noting that accumulation of ant species on islands appears to be accelerating with globalization [83] especially on islands inhabited by people. However, there is more to ants on islands than just their propensity towards invading new territories.

Morrison's (2016) excellent review of the ecology of ants on islands [117] elucidates many trends of these organisms, summarized and supported below. Ants are functionally ubiquitous on islands, and arrive in new places via flight, rafting, and human transport, or colonization before the loss of a land bridge. Most ant colonization attempts of islands likely fail however, as the earlier arrival of an ecologically similar species can slow or prevent the colonization of future sympatric ones. Hardy species of ants can live even in the intertidal zone, particularly in mangroves, and can block the entrance to their chambers during periods of tidal inundation to survive ([121-123, 171]). Other ants dwell in intertidal limestone on islands by retreating to air pockets during inundation, even surviving hurricanes [116]. Aggressive invasives can exclude each other from portions of islands but can only successfully exclude each other completely from small islands. The identities of the subordinant species of a community can be somewhat predictably based on the identity of the dominant species since each dominant competes more strongly with certain species relative to others. Interspecific competition seems to be the underlying mechanism coupled with dominance to determine community structure. Turnover rate of ant species can vary from 0 to 17% per year and depends in part on the species with certain groups being much more resilient [115, 117]. This rate is lower than that of other arthropods on islands, which probably has to do with the long lifespan of ants compared to their arthropod relatives. Sometimes ant plague outbreaks occur on islands, where there is a population boom and then crash. Usually the boom is one of the five worst invader species, all of which are associated with honeydew producing organisms which may play a role in the event. Endemic species seems to be related to the size of the island in the western Atlantic and Caribbean, which actually have high ant endemism compared to other areas but this may be an artifact of incomplete sampling in more remote areas.

Studies of the natural history and diversity of ants on islands tend to focus on an island interior's vegetated habitats as opposed to dune and beach habitats. Work on New Caledonia, for example, did extensive surveys of 56 sites comprised of rainforest, shrubland, savannah, and thicket habitats, but no beach localities [18]. The same trend occurs in work from India [2], Australia [24], Corsica in the Mediterranean [21], Massachusetts [31], Costa Rica [89], and Japan [92], to name but a few examples. Even on small islands like Surprise Island, a 24 hectare Australian coral atoll, the sampling of a recent study followed the trend of focusing on the interior away from the beaches and dunes [28]. Thus while ants on islands have a healthy amount of research literature, studies of ants on dunes are less abundant.

A study looking at ant populations on islands to test island biogeography Density-Area Relationships (DAR) found that larger islands did have larger populations of ants, although the populations were mostly the European fire ant *Myrmica rubra* (L. 1758) [125] . It is possible this effect on islands is a result of a negative edge effect due to flooding on the shore condensing colonies near the shore that would normally be more dispersed [125]. The authors also not that their study was initially designed to study spiders, and they counted ants as individuals without the ability to appropriately speak to colony density [125].

In a metanalysis of the ants of pacific islands seeking to confirm island biogeography concepts using a global ant distribution database comparing endemic, native, Pacific tramp, and exotic species distribution on Pacific archipelagoes, two heavily important factors were found: isolation and island area [61]. The strongest factor influencing the number of colonizing species appears to be the degree of isolation, while island areas larger than 3500 km^2 were likely to have ant population that could undergo speciation in their model [61]. However, human-mediated introductions of exotic ants to islands seems to have filled empty niches in many cases and reduced the strength of the species-isolation relationship [61]. Island area can also increase the number of both ant-plant species interactions, and interactions with exotic species when plants have extrafloral nectaries while connectedness of networks decreased as island area increased [152].

In some cases where islands are sufficiently isolated, they may not have any ant fauna until humans transport invasive or tramp ant species to them. Take the very isolated Juan Fernández Islands of Chile, where only 3 species of ants, 2 tramp and invasive Argentine ants *Linepthema humile* (Mayr, 1868) were recovered in a survey, all likely transported there by humans [87]. Even minimally human inhabited islands can develop an ant fauna dominated by non-native ant species like Cocos Island, Costa Rica, where tramp ant species were the bulk of the assemblage from coastal areas all the way to high elevations and cloud forest despite never having a permanent human settlement on island [146]. However, the possibility exists that humans are not the main transporting agent, as a mechanism for moving ants from island to island and mainland to island is relocation from via prevailing/trade winds [89].

In summation, larger islands appear to have larger ant populations [125] and can have higher species richness due to more niches to exploit as well as the potential for speciation [61]. There is a need for continued research to better document the geographic distribution and ecology of ant fauna on islands, especially as human disturbance appears to be dampening or altering some of the standard biogeography [61]. Invasive species are of particular concern for islands but are not the only area deserving of focus when studying ant assemblages. Further, while it is understandable that many studies focus on the forested interior, the coastal dunes and sandy shores of islands also merit investigation for invasive, endemic, and bioindicator species. Management or eradication of invasive species is most likely to be successful when problematic organisms are detected early, and shoreline assemblages are somewhat simplified versions of interior assemblages, allowing for inferences about an island as a whole when more inland areas are difficult to reach.

Ants in and around Georgia

Another area where the biodiversity and distribution of ants have been understudied is Georgia. Only two statewide surveys have been published. The first, in 1913, is a list of what has been reduced to 62 species reported for the state [165]. The second by Ipser (2004) described the counties and major habitat types where each of the 96 species collected were encountered [88]. One of the locations for the survey included the coastal dunes of Sapelo, where using a combination of baits and pitfall traps *Apheanogaster miamiana* Wheeler, 1932, *Dorymyrmex bureni* (Trager, 1988), and *Solenopsis geminata* (Fabricius, 1804) were collected. Other work has focused on the distribution of the *Solenopsis invicta* X *richteri* hybrid [70] or noted the presence of the invasive Tawny Crazy ant *Nylanderia fulva* (Mayr, 1862) [73]. Two recent online databases, the Global Ants Database [78] and especially antmaps.org [90] are valuable resources that have begun to catalogue the records from many collections and museums. Several surrounding states have been surveyed, Alabama in 2005 [104], North Carolina in 2012 [77], and quite an extensive bit of work coming out of Florida. Some focus has been given to Florida islands [54, 113, 157], and recently an excellent book has been published that includes both identifying traits and natural history information for every known Florida ant species [55]. While there is some work that has looked at freshwater dunes on the Ohoopee river [105] or *Crematogaster pilosa* on Sapelo Island salt marshes [101], no ant survey focused on Georgia’s coastal areas has been conducted.

Georgia Dunes and Islands

Georgia's historic conservation and management efforts have resulted in a range of ecosystems rich in endemic and charismatic species. Georgia's barrier islands are touted as some of the least disturbed on the eastern seaboard. These dynamic, protected coastal ecosystems serve as nurseries for a host of threatened species. In having relatively intact coastal dune habitats, having the added information of the associated ant assemblage would provide useful information for not just Georgia's but also other dune habitats as a comparative baseline of a healthy coastal area. While little work has been done of the coastal dunes, other complementary habitats in Georgia have been studied.

In Georgia sandhill dunes, a study of effects from a nearby military base found that intermediate levels of disturbance foster the highest levels of species richness compared to more and less disturbed areas [62]. Mallinger (2014) did a fine scale identification of the sand dune vegetation on Sapelo Island, one of Georgia's barrier islands, and opportunistically surveyed insects using suspended sticky cards [106] but did not investigate ground dwelling insects. General dune vegetation can be characterized as mobile foredunes mostly colonized by dune stabilizing sea oat *Unicola paniculate*. The interdunes are mostly dominated by clonal grasses like seashore paspalum *Paspalum vaginatum* and clonal forbs like frog fruit *Phyla nodiflora*, while the back dune is more stable and most plant diverse, with long lived woody species [111]. The morphology and vegetation of dunes on Sapelo and the Georgia coast has been described in a series of papers by Stallins [147-149], and conforms to these general trends in areas that have not been invaded by dune stabilizing vegetation like camphorweed.

Conclusions of main themes regarding insects on sandy shores

Historically, knowledge of insects has suffered from the focus of marine researches being turned outward to the sea while terrestrial ecologists gazed inland to the trees, leaving an unexplored gap in-between. Contrary to previous thought, insects often occur as assemblages of multiple species (i.e. 20-40) on a beach-dune, and as a result are more representative of the state of any particular place than the 2-5 crustacean species often found in the same locality. These organisms partition their niches by 1) utilizing various microhabitats and 2) functioning at different times throughout the day tied to various degrees of thermophily. Coastal areas where these insects live are not a single ecological unit but a series of tightly interconnected biotopes defined by their plant community and characterized by the associated insect species [66]. The insects inhabiting the beach-dune tend to dwell in either the vegetation or wrack, but there are also species in both orders that specialize in open sand habitats. Insect abundance in general peaks in spring and decreases through autumn, especially relative to crustaceans, as does insect species richness [36]. Insect richness and abundance can also both be suppressed due to development on or near beach-dune habitats [36], which is one of the trends that make insects useful as bioindicator species. Insect distributions in these habitats can be linked to plant biomass [36] as well as accumulation and aging of beach wrack [37]. Insects can be adept at niche partitioning so that sympatric species can survive in a relatively harsh environment [39]. The assemblage of beach-dune insect species often has a few dominant members, with others rarely encountered [132]. Insects, especially those living the beach wrack can serve as a vital food source for beach dwelling birds [140], or dune dwelling amphibians and reptiles [153], and as such provide a vital food web link between the marine and terrestrial environments. Eulittorial arthropods feed on or are dietarily subsidized by allochthonous marine inputs (wrack), but terrestrial organisms are not [39], instead feeding on those arthropods [26] to form a food web link between the marine and terrestrial biomes. Insects, especially those associated with beach wrack [141] and vegetation, can be valuable bioindicator species on beach-dune systems, whether its dipterans [15], ants [9, 10, 30, 75, 98, 138], or beetles [33]. The complexity and richness of vegetation in the dune slack could be part of the reason for such a distinction between the food webs of the eulittoral and supralittoral fauna [39, 62], but whenever vegetation is found on a coastal system, it is highly likely that ants will also be present [114]. The density and availability of nearby vegetation to utilize for nest sites and food resources appears related to the density and distribution of some dune nesting ant species [47]. One of the important areas of needed research is better documenting both the distribution and natural history of insects in these habitats so that they can be efficiently and accurately used as bioindicator species.

While insects in these systems are understudied in general, ants in particular are both abundant and understudied [153]. That being said, it appears that many trends apply to both ants and beetles with regards to ecological forces and functions. For instance, both ants [75] and beetles [85] have many species which are adapted to open, sandy habitats. It is important to consider the health of macroinvertebrate communities when working towards sustainable beach management [40] due to their role in linking several ecosystems. In the larger context, protecting ecosystem health and monitoring biodiversity are both areas where continued work and research is needed to better inform our management and decision making regarding ways of dealing with anthropogenic pressures placed on sandy beaches, especially the neglected intertidal zone and closely linked dunes [91].

Multiple challenges are coalescing to exacerbate the need for studies of beach-dune organisms as shown in Hubbard et al.'s (2014) metanalysis of isopod data from southern California [86]. Sea level rise, expanding development and coastal armament, along with beach grooming and raking all affect the upper zone of sandy beaches reducing the habitat of insects and crustaceans that live there. The diversity of species more vulnerable to this habitat loss is most likely insects as Hubbard et al. show in listing 6 vulnerable beetle species compared to 3 crustacean species, but the data are lacking to adequately evaluate the state of these overlooked organisms. Additionally, global and regional trends may mask processes functioning at a local scale to affect biodiversity, and local events may be the stronger driver of biodiversity loss [141]. These trends have led Schooler et al. (2017) to suggest a need for long term ecologically minded studies of these areas to accurately assess sandy beach and coastal dune biodiversity status.

Ants affecting beach dwelling organisms

Ants, as E.O. Wilson has put it, are one of the "little things… who run the world." Practically ubiquitous and contributing a large portion of biomass to most systems, ants, especially invasive ones, have begun to show deleterious effects to many other organisms.

Beach and dune nesting birds, like the threatened Wilson's Plover *Charadrius wilsonia* (Ord 1814) [150] and Least tern *Sternula antillarum* (Lesson, 1847)[95] that nest in Georgia, could be at risk to depredation by ants. Least tern eggs and fledglings have been attacked by fire ants *Solenopsis xyloni* McCook, 1880 and Argentine ants in

California [84]. Ants have been collected at Roseate (*Sterna dougallii* Montagu,1813) and Common (*Sterna hirundo* L. 1758) tern nests, but do not necessarily affect mortality [137]. Marine and shorebirds have also been affected by invasive ants, especially ones that nest in large colonies. Yellow crazy ants *Anoplolepis gracilipes* (Smith, 1857) altered abundances, as well as nesting and foraging behaviors of multiple bird species on Christmas Island [46]. Ground nesting Herring gull *Larus smithsonianus* Coues, 1862 chicks have been observed being swarmed and killed by European Fire Ants (*M. rubra)* on Appledore Island, Maine with surviving chicks having slower growth rates and lower survival probabilities [51]. Even non-stinging ants can be deleterious. A colony of Red-tailed Tropicbirds (*Phaethon rubricauda Boddaert, 1783*) on Easter island were filmed with both adults and chicks being swarmed by the Argentine ant *Linepithema humile,* with chicks undergoing mortality [68].

Red Imported Fire Ants (RIFA) *Solenopsis invicta* have a notorious [5, 169] but debated [93, 151] effect on biodiversity. RIFA have been noted as a contributing factor in the decline of amphibian [23] and reptile populations across the globe, even when only present in moderate abundance [6]. Ants have been implicated in cryptic extinction events, where non-charismatic species like the Pacific skink *Emoia impar* (Werner, 1898) on the Hawaiian Islands was lost without notice, likely due to *Pheidole megacephala* [67]. Even in cases where outright mortality has not occurred, RIFA can create deleterious behavioral effects in reptiles depressing population levels [44] and altering behavior[96, 97]. Gopher tortoises *Gopherus polyphemus* Daudin, 1802 had decreased nestling and hatchling survival due to RIFA [59] which seem to be attracted to the nest mucous and moisture females deposit with the eggs [60]. Broad-snouted Caiman *Caiman* *latirostris* Daudin, 1801 have reduced nest success in the presence of RIFA due to hatchling depredation and prevention of parental care when mothers are attacked and driven from nests [107-109].

Sea turtles are also possibly at risk from ant depredation. Much of the literature on this seems to only have data from surveys of turtle nesting beaches with actual reports of ant induced mortality events, however. Loggerhead *Caretta caretta* (L. 1758) and Green *Chelonia mydas* (L. 1758) sea turtle nesting beaches in Florida have been reported highly infested with RIFA [4]. The tropical fire ant *Solenopsis geminata* has been reported as a risk for sea turtles on Central American beaches [163] and in the U.S. Virgin Islands [160]. RIFA have been bait collected at staked sea turtle nests in Florida, along with 21 other ant species [159]. Loggerhead hatchling mortality due to RIFA has been observed in Florida [127] but does appear to be difficult to document. Ants can build entire colony nests inside of the Hawksbill sea turtle *Eretmochelys imbricate* (L. 1766) egg chamber and depredated both eggs and hatchlings [43]. This is not necessarily just an ant phenomenon, as multiple orders of insects have been recorded in sea turtle nests [14, 126]. RIFA have not been observed to directly depredate Loggerhead eggs, but can envenom them rendering the eggs unviable [56]. However, RIFA have been observed depredating Loggerhead hatchlings once they emerge [118]. More data, particularly more direct data is needed to get a more accurate understanding of how ants could be affecting these beach nesting organisms.

Conclusion

Georgia, having one the most pristine coastlines on the eastern coast of the United States with islands like Sapelo that have a well described dune morphology and plant assemblage, contains ideal islands to document the ant assemblage as well. In doing so, many of the trends mentioned in this paper could be further explored and possibly tied together. Georgia's broad, dissipative, gently sloped, fine sand beaches should have high abundance and diversity of small organisms based on the research of the likes of Defeo and Barboza. A coastal survey would provide a link between the work done inland within the state as well as both further north and further west of Georgia documenting coastal ants. At the same time, studying the Georgia ant assembly could add another toolkit through locating bioindicators for the team of organizations working to manage and protect the coastline. *Solenopsis invicta*, since its introduction at Mobile, Alabama has expanded eastward [25], with Georgia's barrier islands being a last possible invasion front for these notorious invaders. Much could be gleaned from studies looking at differences in contemporaneous island ant assemblies if they are in different stages of invasion, but we cannot know if this is the case without surveying these islands. Georgia also harbors multiple endangered animals that nest on its barrier islands, and better understanding the ants on those islands, invasive or not, could help inform our understanding and management decisions of coastal organisms. Ultimately surveying the ants on the sandy shores of Georgia's barrier islands would help us better understand those organisms, those habitats, and our world.

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CHAPTER 2

Formicidae species present on the dunes of Georgia's barrier islands

Insects in general and ants in particular have been understudied on coastal sandy dunes and beaches. Textbooks on coastal systems, as recently as 1990, taught that insects failed to establish on beaches [6], however more current work has shown that both beetles [9] and ants [7] are capable of dwelling in challenging beach and dune environments [4]. Insects have been suggested as possible bioindicators in coastal ecosystems [13], including dune dwelling ants [7, 15] because they display microhabitat specialization and are easy to collect. Additionally, healthy ecosystems tend to have high ant species richness [1, 2], a principle reasonable to apply to island and coastal dune ecosystems.

A baseline of the organisms present in a system must be established in order to use species as bioindicators and only a handful of studies have investigated the presence of ants on dunes. Dune-dwelling ants have been shown to be a critical component of vertebrate food webs in Cape Cod [18], and formicide diversity can be high in disturbed coastal areas that have undergone substantial development such as Nantucket island [11]. Chen et al.'s work in Mexico collected 121 species of ants in dune habitats [7]. To date, no surveys of ants in Georgia have focused on coastal dunes.

Ant diversity in Georgia has been examined in two, separate, statewide and one regional survey. A list of species compiled in 1913 reported 72 species [19] which was later reduced to 62 through taxonomic revisions and contains little information other than presence. A 2004 survey catalogued ground-dwelling ants in relation to Georgia's major land resource areas, reporting 96 species [14]. The inland dunes along the Little Ohoopee River have also been surveyed, with 77 species reported [16]. The current survey adds to the knowledge of ants specific to the coastal dunes of Georgia's barrier island ecosystems as well as the state.

Methods

Study Sites

The barrier islands of the Georgia coast are considered some of the least developed islands along the entire Atlantic coast of the United States [5]. Cumberland, Sapelo, and Little St. Simons islands were surveyed during the summers of 2016 and 2017. The islands were of particular study interest due their protected nature but varied degrees of remoteness and development. Cumberland is a national park and wilderness area. Little St. Simons (LSSI) is a private island under the guidance of the Little St. Simons Ecological Advisory Council. Sapelo is managed through the Department of Natural Resources (DNR) and harbors both the Sapelo Island National Estuarine Research Reserve as well as the UGA Marine Institute. All three islands are only accessible by boat or aircraft but vary in degree of remoteness, with LSSI being adjacent to the more developed St. Simons and Sea islands while Sapelo has a small historic community but is the most isolated. While the islands have some degree of historic human inhabitation and land use, none of the study islands have undergone major development characteristic of a coastal city like Savannah, Ga or the more touristed Jekyll Island.

Collections on each island occurred on the primary and secondary sandy dunes adjacent to the beach. Each island contains central maritime forest habitat, predominantly composed of pine or live oak, which transitions into marsh, estuary, or dune and beach habitats. Both Cumberland and Sapelo have well studied geology and plant communities (e.g. [3, 5, 17]). The commonly encountered plant species on the dunes where ant collection took place are listed in

Table 2.1, with grass identifications from Mallinger (2014) [17].

The islands were selected for this study due to their relatively undeveloped condition and the corresponding sea turtle nesting populations that were of interest to additional study projects.

Sampling Methods

Island dunes were surveyed for ants that would recruit to hot dog protein baits during the summers of 2016 and 2017 on Cumberland, Little St. Simons and Sapelo islands. Initial pilot sampling in 2016 led to an established 2017 protocol. Our plot design (Figure 2.1) consisted of 21 traps along the vegetation edge of the primary dune parallel to the shoreline, with a transect of 3 traps running perpendicular to the shoreline into the dune interior every 50 meters for a total of 36 traps, per plot, during a sample period. Traps were spaced 10 meters apart, resulting in a 200- X 30-meter grid. The vegetation edge was preferentially sampled because that edge is often the indication for beach-nesting vertebrates that it is safe to nest. Our plot design allowed for investigating ant activity between this edge boundary and the more densely vegetated dune interior. In order to sample ants but prevent attracting problematic vertebrate scavengers, traps were placed for 3 hours and then collected. A morning (06:00-09:00), mid-day (12:00-15:00), and early evening (18:00-21:00) sample was taken for each plot.

Species were identified using Joe MacGowan's online key and the collection at the University of Georgia Museum of Natural History with the help of Dr. E. Richard Hoebeke. Ben Gochnour and Doug Booher also assisted in confirming identifications.

Results

There were 2,458 traps out of 4,863 placements that provided evidence of recruitment activity. We collected 28 ant species through bait sampling, and an additional species was collected from collaborators gathering ants found in sea turtles nests (Table 2.2). Voucher specimens were deposited at the Georgia Museum of Natural History at the University of Georgia. Six species: *Solenopsis invicta* Buren 1972, *Forelius pruinosus* (Roger, 1863), *Pheidole morrisii* Forel 1886 , *Dorymyrmex bureni* (Trager 1988), *Pheidole bilimeki* Mayr 1870, and *Solenopsis globularia* (Smith, 1858) made up the majority of the collected assembly, combining for 97.18 % of total abundance and 90.47% of total incidence in the 2017 survey.

Discussion

The total number of species collected is lower than similar studies due to the choice of a single, targeted bait sampling method, which was done to collect ants that would potentially recruit to a vertebrate nest. However, the 29 species collected and Sapelo's corresponding iChao2 estimator [8] of 36.6 ± 2.36 s.e. imply that Georgia's barrier islands harbor a diverse ant assemblage. Additionally, our collected assembly is consistent with the few other coastal dune surveys in collecting most species rarely and a small subset of species making up the majority of the ant abundance (e.g. [7, 9]).

Four of the species collected are new or recently encountered published records for the state. *Cardiocondyla venustula* Wheeler, 1908 was first collected in Georgia in 2015 [12]. *S. globularia* is a new record for the state but commonly occurs in sandy soils in Florida [10]. *Pheidole navigans* Forel, 1902 was previously reported as *Pheidole moerens*, with which it was recently synonymized. *Dorymyrmex reginicula* (Trager, 1988) may have previously been erroneously reported as *Dorymyrmex insanus* (Doug Booher, personal communication).

The assemblage collected in our study is similar to the species assemblage collected at the Ohoopee River Dunes [13], where 15 of our 29 species co-occur and all genera we collected were found. The overlapping assemblages, combined with the larger array of sampling techniques used to collect 77 species in their study implies that the dunes and island ecosystems of Georgia harbor a diverse ant assemblage worth further exploration. Additionally, the presence of new records like *S. globularia* and endemic species like *Pheidole adrianoi* Naves 1985, indicate the potential of the barrier islands to harbor unique insect fauna or possibly serve as a refugia for species driven from the mainland by invasive species (e.g. *S. invicta*) or stochastic events. The presence of multiple newly encountered exotic species also highlights the need for monitoring of these protected areas for potential introductions of community-altering invasive and tramp species.

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CHAPTER 3

Ant assemblages and ecology of Cumberland, Little St. Simons, and Sapelo: Islands at various stages of invasion

Introduction

Insects on coastal dunes are understudied but an emerging area of interest. Beetle diversity in sandy dune ecosystems often exceeds the crustaceans commonly sampled to assess beach and their associated dune habitats [6, 8-17]. Several North American studies have shown a similar species richness in dune dwelling ants, with a specious assemblage dominated by a smaller subset of abundant ant taxa [7, 25, 48, 51]. Mourglia et al. (2015) reported Hymenoptera prefer dune habitats, while beetles occupy the open sand of the beach [44], although from personal observation there seems to be a wide degree of overlap between the two.

Researchers working on dune dwelling ants and beetles have noted that those species prefer particular microhabitats in the challenging dune climate suggesting them as good candidates to serve as bioindicators for the condition of the ecosystem [39]. This can be particularly the case when disturbance [7], development, or tourism [18] occur in a sandy beach habitat, with insect species richness potentially serving as a proxy for overall habitat health in ephemeral and challenging to study coastal areas. However, before species can serve an indicator function, the composition and distribution of the assemblage must be determined, which has not been accomplished for insects in many sandy dune systems.

The dune habitat is naturally dynamic. Storm systems are capable of altering the coastal shores plant community [41], and thus the associated insect assemblies. Strong winds and coastal currents make barrier islands famously mobile if they are not anchored by human development. This tendency towards disturbance makes a sandy shore ecosystem vulnerable to invasion by species, like *Solenopsis invicta* Buren, 1972, adept at exploiting disturbed areas [53]. Further, coastal port cities serve as an entry point for the mobile species transported by human commercial activity. An additional benefit of investigating the ant communities of coastal areas is to provide monitoring for tramp and invasive ant species that have an increased likelihood of introduction with globalization.

Invasive ant species are recognized as potential deleterious components of coastal communities affecting trade, agriculture, tourism, recreation, and charismatic endangered species. Coastal Georgia has a uniquely pristine barrier island system, with some of the least developed islands along the entire eastern coast of the United States. However, two of the busiest and fastest growing sea ports are on the Georgia coast at Brunswick and Savannah.

Despite the ecological and economic importance of ants, the distribution and assemblage of ants in Georgia is understudied. Two statewide surveys have been performed, a list of species published in 1913 [57] and a University of Georgia survey published in 2004 [35]. To date, no comprehensive survey of the Georgia coast has focused on ants. However, increasing transit through areas like ports is accelerating the rate of ant invasions, especially on islands [23, 24, 33]. Thus, a need exists to document the current assemblage of ants on islands as well as monitor coastal areas for potential invasive introductions.

There are multiple invasive ant species of concern for Georgia. The range of the notorious Red Imported Fire Ant (RIFA) *S. invicta*, known for occupying disturbed habitats [52], has expanded eastward since its introduction at the port of Mobile [5] with Georgia's barrier islands being a last possible eastern invasion front for the species. More recently, the Tawny Crazy Ant *Nylanderia fulva* (Mayr, 1862) has arrived in Georgia [29], and has begun displacing RIFA colonies at the port of Savannah (Gochnour and Suiter, personal communication). Another ant species joining RIFA on The World Conservation Union (IUCN) list of 100 worst invasive species [38], *Pheidole megacephala* (Fabricus, 1793) is established in Florida [21] but has not yet been documented in Georgia. Each of these ant species are known pests, causing distress to homeowners, decreasing diversity of invertebrates [37, 59, 60], and putting additional pressure on vulnerable vertebrate populations.

Georgia's coast has traditionally been a protected breeding area for multiple at-risk species. The threatened Piping Plover *Charadrius melodus* and endangered American Oystercatcher *Haematopus palliates* both nest on Georgia's sandy shores, as does the endangered Loggerhead Sea Turtle *Caretta caretta*. Ants have been shown to depredate ground nesting adult birds and their hatchlings [28, 40], especially if the birds nest in large colonies like terns [34] or gulls [20]. Piping plovers often join colonies of terns to nest. Reptiles are more at risk [2], with loggerhead eggs capable of being envenomed by RIFA [22] and hatchlings being depredated [1, 43]. Direct observations of these types of interactions are rare and difficult to obtain and that makes documentation of ant interactions with coastal nesting vertebrates important.

Joining each of these areas of interest, this project set out to survey more remote barrier islands of the Georgia coast to document the current ant assemblages and investigate their island biogeography. The survey simultaneously served to monitor for known or potential invasive ant species and to document observed ant interactions with loggerhead sea turtle nests during the sea turtle nesting season.

The survey had 3 objectives: 1) Identify the ant species attracted to protein baits on the dunes of Georgia's barrier islands. 2) Quantify environmental characteristics that affect the distribution and composition of those ant assemblages. 3) Examine if invasive ant species are affecting native ant assemblages?

Methods

Research Sites: Cumberland, Little St. Simons (LSSI), and Sapelo islands were surveyed for ants that would recruit to protein baits. The islands were selected for study due their protected nature but varied degrees of remoteness and development. Cumberland is a national park and wilderness area. Little St. Simons is a private island under the guidance of the Little St. Simons Ecological Advisory Council. Sapelo is managed through the Department of Natural Resources (DNR) and harbors both the Sapelo Island National Estuarine Research Reserve as well as the UGA Marine Institute. All three islands are only accessible by boat or aircraft but vary in degree of remoteness, with LSSI being adjacent to the more developed St. Simons and Sea islands while Sapelo has a small historic community but is the most isolated. Each island has a large portion of Georgia's nesting loggerhead sea turtle population from May through October, with 48.68% (1,051 of 2159) of the loggerhead nests from the 2017 nesting season deposited on one of the three islands' beaches (Georgia Sea Turtle Cooperative, personal communication).

Trap Design: A trap was needed that was both durable enough to endure the harsh beach environment to be reusable and designed in such a way that non-target beach organism were not inadvertently collected. The trap (Figure 3.1) design consisted of nested PVC sleeves with 6 holes drilled so that the trap can be rotated into an available and fully closed position. The trap could be opened at one end to extract organisms and load bait. A 1.27 cm (1/2") long ring was cut of 3.175 cm (1-1/4") diameter PVC and affixed with PVC cement inside a 1-1/4" slip cap. A 2.54 cm (1") diameter PVC pipe cut to 16.5cm in length was inserted into the slip cap, guided by the ring, and affixed with PVC cement. A 3.175 cm (1- 1/4") PVC pipe, cut to 15.24 cm (6") in length, was inserted into the dried slip cap. A series of three holes spaced roughly 3.81 cm (1.5") apart along the length of the apparatus were drilled into both pipe lengths simultaneously using a 3/16-inch drill bit. A parallel set of three holes was then drilled, spaced roughly 5 cm (2") in circumference away from the first holes. Finally, a second slip cap was attached to the apparatus, but left uncemented to provide an accessible opening.

Coinciding with the loggerhead nesting season, during the summers of 2016 and 2017, the dunes of each island were surveyed for ants using hot dog protein baits. Initial pilot sampling in 2016 led to an established 2017 protocol. Our plot design (Figure 3.2) consisted of 21 traps along the vegetation edge of the primary dune parallel to the shoreline, with a transect of 3 traps running perpendicular to the shoreline into the dune interior every 50 meters for a total of 36 traps during a sample period. Each trap was spaced 10 meters apart, resulting in a 200- X 30-meter grid. The vegetation edge was preferentially sampled as that edge is often the indication for beach-nesting vertebrates that they are far enough inland to nest safely. Our plot design allowed for investigating the difference in activity between this edge boundary, where vegetation first occurs, and the more densely vegetated dune interior.

A total of 10 plots were sampled in 2017 on each island to survey the breadth of each shoreline. In order to sample local ants but prevent attracting problematic vertebrate scavengers, traps were placed and collected after 3 hours. A morning (06:00-09:00), mid-day (12:00-15:00), and early evening (18:00-21:00) sample were taken for each plot. Traps were bagged upon collection and frozen, with all insects collected stored in 100% ethanol and transported to UGA for identification and counting. Areas within a grid that were in proximity to an active sea turtle nest or where the habitat transitioned to another habitat type (e.g. pine forest or marshy grassland) were not sampled.

During the 2017 sampling, within each plot each trap position was flagged the day before sampling to ensure consistent bait placement between time periods. Environmental habitat data were collected at each plot at each trap position during flagging. A square-meter-grid with a rope lattice of 100 squares was used to determine percent ground cover (consisting of vegetation, beach wrack, and woody debris) around each trap. Relative humidity, air temperature, and wind velocity were collected with an anemometer placed at a height of 28-cm using a tripod, and ground temperature was recorded using a handheld laser thermometer at each plot position. When baits were placed or collected, the same set of environmental data were collected for the corners and mid points of each plot.

Statistical Analyses

Assemblage Richness Analysis: The incidence of encounters (presence of species *x* in a trap = 1 incidence of species *x*) were recorded for use in species richness analyses as recommended by Gotelli et al. (2011) because "[t]he raw count of the number of workers may dramatically overestimate the abundance of colonies of some species" [30]. Incidence counts of each species found in each plot in the 2017 sampling were used to perform Bray-Curtis ordination [3] to establish dissimilarity distance between each plot on each island. The resulting points were plotted in an NMDS (nonmetric multidimensional scaling) plot for cluster analysis with ordination and tested for significance with ANOSIM (analysis of similarities) performed in R using the *vegan* package [45]. Once clusters were recognized, indicator analysis was performed in R using multilevel pattern analysis (multipatt) via the *indicspecies* package [19]. See Appendix 1 for R code.

Modeling: Abundance counts (total number of ants for each species in a trap) were used for evaluating variation between islands for each species. A generalized linear mixed modeling approach via the GLIMMIX procedure [49] in SAS 9.4 was constructed to test for variation in the abundance of each species between islands, with placement of the bait in the dune edge or interior, the time of day, percent ground cover, and their various interactions all serving as components of the model. The model was fit to a negative binomial distribution and utilized a log link function. Plot and time of day were treated as random effects. See Appendix 1 for the code used to construct the model. Each commonly encountered species was modeled, as was a combined count of all rarely encountered species.

Results

Assemblage Richness: Twenty-eight ant species from 14 genera were collected during the survey (Braman and Forschler 2018). In 2017, 209,724 ants were collect in 1,304 encounters from 3,099 traps. Between the 2016 and 2017 surveys, altogether 12 species were encountered on Little St. Simons, 19 on Cumberland, and 22 on Sapelo with at least one species solely collected on each island.

Six species (*Dorymyrmex bureni* (Trager, 1988), *Forelius pruinosus* (Roger, 1863), *Pheidole bilimeki* Mayr, 1870, *Pheidole morrisii* Forel, 1886, *Solenopsis gobularia* (Smith, 1858), and *S. invicta*) were defined as commonly encountered species when total abundance was ≥ 2,881 individuals and total incidence was ≥ 31 for 2017 (Table 3.1, Figure 3.3). Three clusters were identified in NMDS cluster analysis, corresponding to each island (Figure 3.4). Analysis of similarities (ANOSIM) between island assemblages reported dissimilarity (R = 0.569, p =0.001). Indicator analysis identified 5 species in 3 groupings that were significant indicator species (Table 3.2). Sapelo had higher recruitment of ants to baits, and the proportion of the assemblage on each island comprised of *S. invicta* differed dramatically (Figure 3.5). Foraging intensity (individuals collected/encounters) differed between each of the commonly encountered species, with average individuals per encounter by species being: *S. invicta* 275, *D. bureni* 82, *Ph. morrisii* 150, *F. puinosus* 248, *Ph. bilimeki* 141, and *S.globularia* 63 (Figure 3.6).

Modeling: Each of the 6 commonly encountered species had factors or interactions of factors within our model that significantly affected abundance, although they varied by species (Table 3.3). Further, the model identified 2 distinct island activity groupings for several commonly encountered species: *F. pruinosus*, *Ph. morrissii*, and *D. bureni* were more active on Sapelo, while *S. invicta* was most active on LSSI (Table 3.4). Modeling also indicated a statistically significant separation (Alpha = 0.05) in activity between the dune edge and dune interior for each of the 6 common species ((*Dorymyrmex bureni*, *Forelius pruinosus*, *Pheidole bilimeki*, *Pheidole morrisii*, *Solenopsis gobularia*, and *S. invicta*), although no such separation was found for the grouped uncommonly encountered species. Several, but not all, commonly encountered species had separations in abundance relative to day period: *Ph. morrisii* more active in the morning and evening, *D. bureni* more active in the mid-day, and *S. invicta* more active in the early evening (Table 3.5).

Discussion

This study targeted ants that recruit to a meat bait in order to collect species that could potentially depredate beach nesting vertebrates. The resulting ant assemblage consisting of many infrequently encountered species with a subset of commonly encountered species coinciding with other studies that investigated ant communities on coastal dunes [7, 25].

The cluster, ANOSIM, and indicator analyses, show the ant assemblages on each island to be distinct, especially Sapelo. The Cumberland island assemblage's grouping both with Sapelo and Little St. Simons in the indicator analysis implies an intermittent assemblage between the Sapelo and LSSI. This intermediate state can be observed by the equivalent species richness between Cumberland (19) and Sapelo (22) but the presence of *S. invicta* on Cumberland and LSSI (Figures 3.4 & 3.5). The modeling approach identifyied various sets of 2 groupings by island for each species (Table 3.4) and corroborates that the island assemblages are distinct but overlapping, both in species composition and activity.

The question naturally arises as to what factors affect those ant assemblages? Classic island biogeography would suggest that Little St. Simons which lies between Cumberland, to the south, and Sapelo, would have an assemblage overlapping with both islands. Cumberland, a much larger island with nearly 5 times the coastline of the other islands, should be the most species rich. Yet Sapelo had the highest encountered diversity (22 species) while the similarly sized Little St. Simons recorded roughly half the species (12) of the other islands.

The main contrast between island assemblages is the proportion occupied by *S. invicta*, especially the near absence of that species (<1% of assemblage) on Sapelo (Figure 3.3). Combined with the indicator analysis result that *S. invicta* is representative of the combined Cumberland and LSSI ant assemblage grouping (Table 3.2), it seems likely that *S. invicta* is affecting ant assemblages of those islands. Invasive [4, 37, 42] or dominant [26] ant species can reduce species richness to homogenize ant assemblages. In areas where *Pheidole megacephala* was eradicated, ant abundance and species richness increased above pre-eradication levels [32] indicating invasive ants do have strong but mitigatable effects on ant assemblages. While there has been some debate as to whether *S. invicta* affects ant diversity, the introduction of *S. invicta* to an assemblage can devastate the local ant community [46]. During invasion, *S. invicta* populations tend to be initially abundant before crashing [54], resulting in a small subset of native ants coexisting with *S. invicta* [31]. The Georgia barrier islands, with their differing degrees of *S. invicta* presence and similarly differing ant assemblages, are likely undergoing various stages of this disruption and stabilization.

Despite the debate regarding the extent to which *S. invicta* can drive species loss [36, 50], it seems clear they can impact communities of both ants and vertebrates upon invasion [54]. The other commonly encountered ant species from our surveys are likely candidates for survivorship to stabilization, namely *D. bureni, Ph. bilimeki, Ph. morrisii,* and *S. globularia*. All of the commonly encountered species from our survey appear to be species that are relatively heat tolerant and adept at exploiting microhabitats with sandy soils [21]. If ants follow the trends of the better studied dune dwelling beetles, the dune populations are likely partitioning into environmentally specific microhabitats.

Several of the commonly encountered species may be achieving subdominance through niche partitioning by specializing or monopolization of plant extrafloral nectaries and associated honeydew producing hemipterans as seen in a community in Brazil [27]. Our modeling showed vegetation and ground cover significantly affect *Ph. morrisii* activity (Table 3.3). Further, all commonly encountered species had significantly higher activity in the dune interior, relative to the edge (Tables 3.3) which is likely due to dense clusters of vegetation in the dune interior. There are multiple plant species that produce extrafloral nectaries on the Georgia barrier islands (e.g. Seaside morning glory *Ipomoea pes-capae* (L) and Eastern prickly pear *Opuntia humifusa* (Raf.)), resources which each of the commonly encountered ant species could utilize. Ant behavior exploiting these resources may be more extreme on islands, as water stress, a relatively constant occurrence on a beach-dune system, can strengthen mutualisms between both ant-plant and ant-hemipteran interactions [47]. Further, *D. bureni* and *F. pruinosus* both can have their aphid tending mutualism disrupted in the presence of *S. invicta* [58], indicating the assemblages of each island could be disrupted by continued or increased *S. invicta* presence.

The concern over deleterious effects of *S. invicta* should be tempered, as their presence does not necessarily imply ensuing disruption. Island environmental conditions may limit the success of otherwise notorious invasive species, as seen with the relatively intact assemblage on Madeira 150 years after acquire 2 notorious invasive species [56]. However, introduced species can become dominant on islands [55]. The abundance of workers in *S. invicta* colonies makes it challenging to parse the abundance between islands. Yet, the significantly higher frequency of recruitment (higher incidence, Figures 3.4 and 3.5) of ants on Sapelo implies something is depressing the abundance or activity of ants on the other islands, possibly *S. invicta*.

Observationally, it appears that on the islands where it is present (Cumberland and LSSI), *S. invicta* has become dominant, with *Dorymyrmex bureni* functioning as a subdominant species. However, on Sapelo, the data indicated a 3-way co-dominance between *D. bureni*, *Forelius pruinosus*, and *Pheidole morrisi* (Figure 3.4). It is possible these species accomplish niche partitioning via temporally separated activity with *Ph. morrisii* more active in the morning, *D. bureni* more active at mid-day, and *S. invicta* more active in the early evening (Table 3.5).

While our model was able to show these species differentiating their activity throughout the day, *F. pruinosus* does not. Thus while *D. bureni* and *Ph. morrisii* could be foraging at times when *S. invicta* is not present to avoid competitive encounters with *S. invicta*, by being active throughout the day *F. pruinosus* would likely encounter *S. invicta* where their colony territories overlap. Due to *S. invicta's* aggressive nature, such encounters could potentially result in raiding and extirpation of *F. pruinosus* by *S. invicta* in those areas. This lack of temporal specificity and resultant increased chance of encountering *S. invicta* may be one reason for *F. pruinosus'* absence on islands where *S. invicta* has invaded and become the dominant species and warrants further investigation.

Pheidole adrianoi was an uncommonly encountered species, but also an indicator representative of the Cumberland and Sapelo assemblage grouping (Table 3.2). The species is endemic to Florida, Georgia, and Alabama, and its presence implies the assemblages of both islands contain a relatively intact native assemblage. Additionally, *Solenopsis geminata* was collected solely on Sapelo. At a localized level *S. invicta* distributions tend to not overlap with *S. geminata* [52] which is thought to be native to the southeastern US, giving credence to the notion that Sapelo is relatively untouched by *S. invicta*. The presence of *P. adrianoi* on both Cumberland and Sapelo, combined with its absence on LSSI, add another line of evidence that *S. invicta* may have begun extirpating local fauna on LSSI but not yet become well enough established to do so on Cumberland.

Conclusions

We can conclude 1) The dunes of Georgia's barrier islands harbor a rich ant assemblage with significant differences among islands. 2) Our survey and modelling indicated there were significant effects of time of day, ground cover, and position within the dune on ant activity. While the current study has limited ability to identify particular factors causing these trends, our data indicate it would be a fruitful avenue for further inquiry. 3) The invasive ant *Solenopsis invicta* has reached the barrier islands of Georgia, however, each of our survey islands appear to be in different stages of invasion. From the relatively depauperate assemblage on Little St. Simons, combined with the abundance of *S. invicta* there compared to Cumberland and Sapelo, it seems likely that LSSI has been under invasion pressure from *S. invicta* for the longest time. Cumberland has been invaded as well, however, its higher richness and lower *S. invicta* abundance imply that it has been invaded more recently or has other factors mitigating the impact of *S. invicta* on the ant community. Sapelo appears to be unaffected by *S. invicta* so far, however *S. invicta* was recovered in small numbers there as well. Together, these lines of evidence suggest that the study islands are at various stages of invasion and would provide a well contained set of real world laboratories for further study of the ecology of invasion island biogeography.

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CHAPTER 4

Ants encountered in sea turtle nests and ant related trends to sea turtle hatchling success

Introduction

Sea turtles face a wide range of natural and anthropogenic challenges during adult female nesting until hatchling emergence. Amongst the many well documented pressures like foraging mammals and inundation of eggs by water, a potential emerging concern is the introduction of the Red Imported Fire Ant (RIFA), *Solenopsis invicta* Buren 1972. *S. invicta's* range extends throughout the southeastern United States [4] and it's spread to the Caribbean [17] increasingly overlaps with habitats where sea turtles nest.

Reptile nests and hatchlings in general are vulnerable to fire ants. The presence of RIFA depresses both nestling and hatchling survival for Gopher tortoises, where although RIFA cannot penetrate the eggs RIFA can depredate up to 50% of piping hatchlings [7]. RIFA have been found in broad-snouted Caiman *Caiman latirostris* nests [10], where they are thought to lower hatchling survival [11] and depress hatch success [12]. Research with freshwater turtles found that *S. invicta* can kill imperfectly-shaped eggs as well as hatchlings that attempt delayed emergence [3].

Documentation of insects depredating sea turtle eggs and hatchlings is sparse. What evidence exists is mostly inferential and begs the question of what was observed, actual predation or scavenging. RIFA are present on sea turtle nesting grounds in Florida and will depredate freshwater turtle eggs [1]. Green *Chelonia mydas* and loggerhead

Caretta caretta sea turtle nests have been reported to be infested, and eggs damaged, by tenebrionids and dipterans [2]. Both dipterans and formicids have been documented reducing hawksbill hatch success, especially in nests close to vegetation [5]. These findings have been corroborated by a study which found loggerhead nests more likely to be infested by invertebrates the closer to vegetation and the smaller the sand grain size [13].

Where evidence of depredation is not present, stinging ants still have the potential to cause deleterious effects. RIFA, in a lab setting, have been shown to induce loggerhead egg mortality via envenomation [6]. Sea turtle hatchlings that remain in the nest chamber before emerging from the sand could be vulnerable to ant predation similar to events seen with gopher tortoises and caiman [7, 10-12].

Increasingly, several species of fire ants have been proposed as potential risks to sea turtle nest. The tropical fire ant *Solenopsis geminata* (Fabricius, 1804) was reported present at sea turtle hatcheries in El Salvador [18] and both *S. invicta* and *S. geminata* were found on turtle nesting beaches in St. Croix [16]. RIFA were first documented in Loggerhead sea turtle nests at Cape San Blas in 1995 with hatchling mortality documented 2 years later [14]. Researchers in Florida placed baits to document ant presence. Twenty-two ant species were collected from baits placed on marked sea turtle nests in Florida, with *S. invicta* being the most commonly collected species [15]. Further, they found that 93% of nests within 2-m of the dune vegetation had ants present [15].

The concern about potential deleterious interactions between ants and nesting sea turtles led us to investigate the current situation in Georgia. Georgia has some of the most protected and well-kept barrier islands along the Atlantic coast of the United States. Predominantly Loggerhead sea turtles nest on Georgia's beaches from May through October.

Our study had 2 objectives:

1) Document interactions between ant species and sea turtle nests along the Georgia Coast.
2) Determine if sea turtle nests with ants resulted in lower clutch size, hatch success, or emergence success for those nests compared to the population as a whole.

Methods

In the summers of 2016 and 2017, collaborators from the Georgia Sea Turtle Cooperative (GSTC) collected ants they encountered when investigating disturbances (i.e. raccoons or coyotes depredating a nest) or excavating hatched sea turtle nests along the Georgia coast. Technicians for each project within the GSTC patrol beaches each morning of the sea turtle nesting season. Nests are monitored until hatch or 70 days have passed, at which point the egg chamber is excavated to determine clutch size (number of eggs), hatch success (proportion of eggs that hatched/clutch size) and emergence success (proportion of hatchlings that exited the nest chamber/clutch size). Ants collected by GSTC technicians were frozen until sent to the University of Georgia for identification.

Cumberland, Little St. Simons, Sapelo, and Wassaw Islands provided nest success data from the 2016 and 2017 sea turtle nesting seasons. All records of nests with known disturbances or causes of reduced success including depredation by mammals and ghost crabs, root growth in the egg chamber, overwash, storm damage or flooding that resulted in the loss of 5 or more eggs were removed from the data set. As Loggerhead clutch size is roughly 119 eggs [8], by selecting 5 eggs as the cut off disturbances resulting in more than 5% clutch loss were removed. The remaining data were analyzed using ACNOVA and regression to investigate the relationship between hatch success and ant presence with clutch size as a covariate, as well as the relationship between emergence success and ant presence with hatch success as a covariate.

Results

The GSTC technicians on 8 islands collected ants during the 2016 and 2017 nesting seasons providing 116 samples representing 14 ant species and 5 samples contained more than one ant species. *S. invicta* was the most commonly encountered species on 5 islands (Blackbeard, Cumberland, Jekyll, Little St. Simons, and Wassaw) (Figure 4.1). *Dorymyrmex bureni* and *Forelius pruinosus* were the most commonly encountered species on Sapelo and Ossabaw islands (Figure 4.1). All species, except *S. invicta,* collected by GSTC are endemic to the southeastern United States.

S. invicta was the most commonly encountered species (40.5%, n=49) followed by *D. bureni* (20.7%, n=25), *F. pruinosus* (10.7%, n=13), and *Pheidole morrissi* (9.9%, n=12). The remaining 10 species were encountered 6 times or less (Figure 4.2).

There were 1500 nests from 2016 and 752 nests from 2017 combined for a total of 2,252 nests in the nest-success analysis data set with 85 nests that reported ant activity. ANCOVA on the response of hatch success to ant presence with clutch size as a covariate found no significant difference. The response of emergence success to ant presence with hatch success as a covariate found both hatch success ($p < 0.0001$) and ant presence ($p < 0.0001$) to be significant as well as the interaction of hatch success and ant presence (p =

0.0219). Regression lines for nests with ants and without ants separate significantly at roughly 50% hatch success (Figure 4.3) with nests with ants exhibiting lower modeled emergence success.

Discussion

The presence of *S. invicta* in sea turtle nests was expected but collecting 13 native species in sea turtle nests (Figure 4.2) demonstrates, for the first time in the southeastern U.S. to our knowledge, that RIFA and native ant species will potentially use sea turtle nests as resources, regardless of island (Figure 4.1). The frequent collection of endemic species in the sea turtle nests indicates that opportunistic native and invasive ant species use sea turtle eggs and hatchlings as food resources.

Currently, the reported incidence of ant encounters in sea turtle nests is small (85 out of 2252, or 3.77% of our data set) relative to more notorious disturbances like raccoons and feral hogs on islands. However, only roughly 1 in 1,000 sea turtle hatchlings reach reproductive adulthood [9]. Thus any management or prevention of ant depredation that results in even minor improvements in initial hatchling survivorship would prove beneficial to sea turtle population growth.

While hatch success appears to not be affected by the presence of ants, the emergence success does trend differently in the presence or absence of ants (Figure 4.3), with lower emergence success in the presence of ants. This trend, combined with the multiple native ant species found in sea turtle nests, implies that both invasive and native ants may be affecting sea turtle emergence success. However, our study design is not able to answer the question of whether ants are directly affecting sea turtle hatchlings, or if they are merely attracted to nests where hatchlings are already having difficulty emerging. Due to the potential benefit to sea turtle recovery efforts if ants can be shown to be a preventable population pressure on sea turtles, the question of whether or not ants in sea turtle nest are actually suppressing emergence should be investigated further.

It is likely that ants foraging in sea turtle nests are mostly opportunistic encounters. However, as sea turtle populations recover and rookeries become more densely covered with sea turtle nests, the likelihood of such encounters with ants could also increase and create a new population pressure for sea turtles.

Conclusion

Both native ant species and *S. invicta* were documented in sea turtle nests on multiple islands along the Georgia Coats. While the presence of ants did not have an effect on nest hatch success rates, sea turtle nests where ants were encountered had a lower emergence success rate. Further research into the interactions between ants and sea turtle nests are warranted as they could help conservation efforts for sea turtles preempt any challenge ants may produce before it fully manifests.

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Table 1.1: Commonly encountered plant species on Georgia barrier island dunes

Common name	**Species Name**
Beach-tea croton	*Croton punctatus*
Bitter panicgrass	*Panicum amarum*
Cabbage palm	*Sabal palmetto*
Camphorweed	*Heterotheca subaxillaris*
Cockspur pricklypear	*Opuntia pusilla*
Eastern prickly pear	*Opuntia humifusa*
Fiddleleaf morning glory	*Ipomoea stolonifera*
Glasswort	*Salicornia spp.*
Narrowleaf silkgrass	*Pityopsis graminifolia*
Pennywort	*Hydrocotyle bonariensis*
Russian thistle	*Kali tragus*
Sea Oats	*Uniola paniculata*
Sea rocket	*Cakile spp.*
Seashore dropseed	*Sprobolus virginicus*
Seaside morning glory	*Ipomoea pes-caprae*
Spanish Bayonet	*Yucca aloifolia*
Wax myrtle	*Myrica cerifera*

Table 1.2: List of ant species collected while surveying the primary dunes. Islands/areas where each species was encountered are also noted by first letter (**C**umberland, **L**ittle St. Simons, **S**apelo, and sea **T**urtle nests), as well as the previously currently thought status for each species in the state.

Species	Islands Present	Status (Native/Exotic/Invasive)
Aphaenogaster flemingi Smith, 1928	C, S	Native
Brachymyrmex depilis Emery, 1893	C, S	Native
Brachymyrmex patagonicus Mayr, 1868	C	Exotic
Camponotus floridanus (Buckley, 1866)	C, S, T	Native
Cardiocondyla venustula Wheeler, 1908	C, S	**Recent record, exotic**
Crematogaster laeviuscula Mayr, 1870	S	Native
Crematogaster pilosa Emery 1895	L, S	Native
Crematogaster pinicola Deyrup and Cover, 2007	L, S	Native
Cyphomyrmex sp. Mayr, 1862	C	Exotic
Dorymyrmex bossutus (Trager, 1988)	T	Native
Dorymyrmex bureni (Trager, 1988)	C, L, S, T	Native
Dorymyrmex reginicula (Trager, 1988)	L, S, T	**New record, native to the southeastern U.S.**[*]
Forelius pruinosus (Roger, 1863)	C, L, S, T	Native
Lasius neoniger Emery, 1893	S	Native
Monomorium minimum (Buckley, 1866)	L	Native
Nylanderia concinna (Trager, 1984)	C, L	Native
Pheidole adrianoi Naves,1985	C, S	Native, endemic
Pheidole bilimeki Mayr, 1870	C, L, S, T	Native
Pheidole dentata Mayr, 1886	C	Native
Pheidole metallescens Emery, 1895	C, S	Native
Pheidole morrisi Forel, *1886*	C, L, S, T	Native
Pheidole navigans Forel, 1901	C, S	**New record, exotic****
Pogonomyrmex badius (Latreille, 1802)	C, S, T	Native
Solenopsis abdita Thompson, 1989	C, S	Native
Solenopsis geminata (Fabricius, 1804)	S, T	Native
Solenopsis globularia (Smith, 1858)	C, L, S, T	**New record, native to the southeastern U.S.**
Solenopsis invicta Buren, 1972	C, L, S, T	Exotic
Solenopsis molesta Emery, 1895	S	Native
Solenopsis pergandei Forel, 1901	C, S, T	Native

[*] **could have previously been reported as *D. insanus***

[**] **could have been previously reported as *P. moerens***

Table 3.1: 2017 counts for the 6 commonly encountered species, as well as a combined count of the remaining 20 uncommonly encountered species sampled during 2017. Data are reported in each cell as *Total Individual Ant Abundance / Total Incidence of Species Encounter*. Columns designate each island, as well as a combined survey total.

Species	Cumberland	LSSI	Sapelo	Total
D. bureni	**8,088 / 124**	**7,410 / 62**	**15819 / 197**	**31,317 / 383**
F. pruinosus	**8 / 2**	**2 / 1**	**36, 654 / 145**	**36,664 / 148**
Ph. bilimeki	**1,055 / 4**	**1,478 / 12**	**1,836 / 15**	**4,369 / 31**
Ph. morrisi	**5,333 / 46**	**1,764 / 17**	**29,367 / 180**	**36, 364 / 243**
S. globularia	**1,227 / 20**	**1,527 / 18**	**127 / 8**	**2, 881 / 46**
S. invicta	**27,462 / 88**	**64,581 / 244**	**75 / 3**	**92,118 / 335**
Uncommon	**341 / 28**	**845 / 27**	**4,725 / 81**	**5,911 / 125**
Total	**43,514 / 363**	**77,607 / 312**	**88,603 / 629**	**209,724 / 1,304**

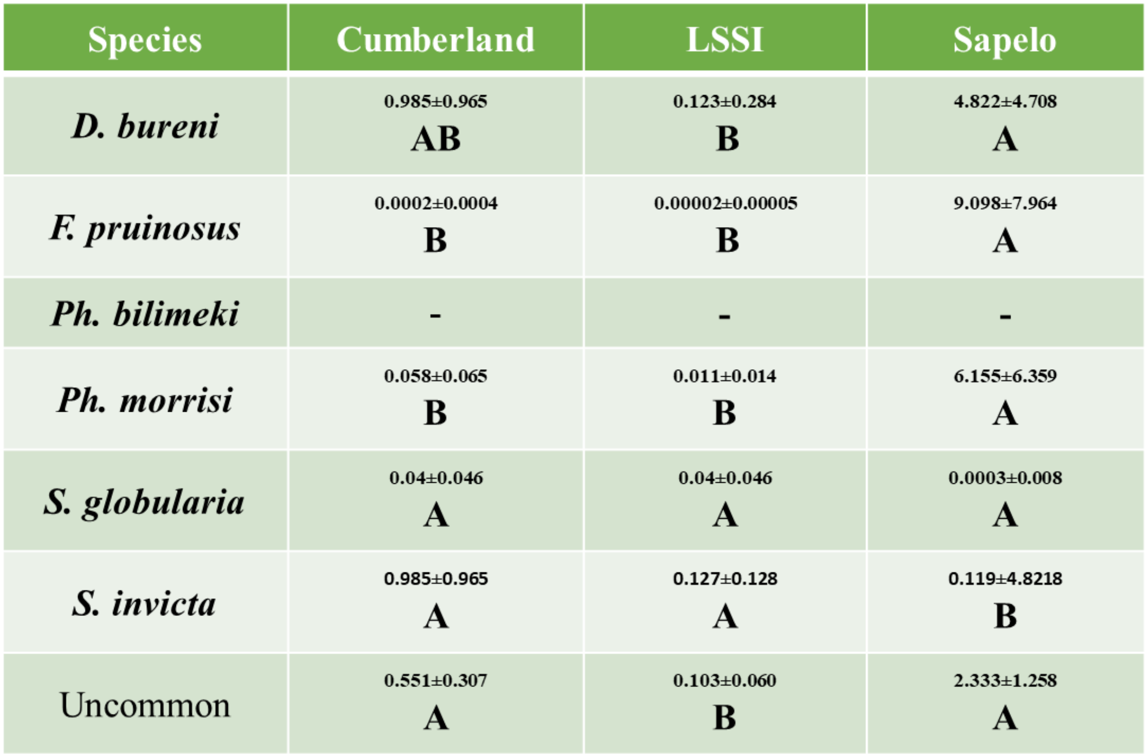
Table 3.2: Indicator Analysis groupings and indicator species. Multilevel pattern analysis determined 3 groupings based on 2017 ant incidence counts. Numbers below species are indicator index values and significance level [55].

Group	Species 1	Species 2
Sapelo	*Forelius pruinosus* (0.990, p = 0.001)	*Crematogaster pilosa* (0.687, p = 0.009)
Cumberland + LSSI	*Solenopsis invicta* (0.996, p = 0.001)	
Cumberland + Sapelo	*Pheidole morrisi* (0.940, p = 0.004)	*Pheidole adrianoi* (0.775, p = 0.008)

Table 3.3 Factors with significant effect on modeled species abundance based on a generalized mixed modeling approach. Island was a categorical consisting of Cumberland, Sapelo, or Little St. Simmons. Edge/Interior represented position of the bait within the dune. Day period was either morning (6:00-9:00), mid day (12:00-15:00) or Early Evening (18:00-21:00). Percent Ground Cover was a combined percentage of vegetation, beach wrack, and woody debris covering the sand. For the combined uncommon species data, day period and its interactions were not included as the model would not resolve when including day period due to the scarcity of encounters. *=p<.05, **=p<.005, ***=p<.0005

Species	**Island**	**Edge/Interior**	**Day Period**	**% Ground Cover**	**Island x Edge**	**Island x Day Period**	**Edge x Day Period**
D. bureni	*	***	***		***		
F. pruinosus	***	*	*				**
Ph. bilimeki		**					
Ph. morrisi	**	***	***	*	***	***	*
S. globularia		**					*
S. invicta	***	***	***		***		*
Uncommon	**		**n/a**	*		**n/a**	**n/a**

Table 3.4: GLMM grouped abundance by island. Values reported are mean abundance per trap per island (n= 3099). Letters designate statistically significantly different groupings. Each grouping is only valid for its row as each model was run on a single species. No seperation occurred and modeled abundance was near zero for *Pheidole bilimeki*.



Species	Cumberland	LSSI	Sapelo
D. bureni	**0.985±0.965** **AB**	**0.123±0.284** **B**	**4.822±4.708** **A**
F. pruinosus	**0.0002±0.0004** **B**	**0.00002±0.00005** **B**	**9.098±7.964** **A**
Ph. bilimeki	**-**	**-**	**-**
Ph. morrisi	**0.058±0.065** **B**	**0.011±0.014** **B**	**6.155±6.359** **A**
S. globularia	**0.04±0.046** **A**	**0.04±0.046** **A**	**0.0003±0.008** **A**
S. invicta	**0.985±0.965** **A**	**0.127±0.128** **A**	**0.119±4.8218** **B**
Uncommon	**0.551±0.307** **A**	**0.103±0.060** **B**	**2.333±1.258** **A**

Table 3.5: Commonly encountered species with significantly different activity by time of day. Numbers reported are modeled abundance per trap per day period ± 1 standard error (n=3099). Letters designate statistically significant different groupings. Each grouping is only valid for its row as each model was run on a single species.

Species	Morning	Mid Day	Early Evening
D. bureni	**0.472±0.287** **B**	**1.753±1.056** **A**	**0.727±0.443** **B**
F. pruinosus	/	/	/
Ph. bilimeki	/	/	/
Ph. morrisi	**0.272±0.190** **A**	**0.041±0.029** **B**	**0.365±0.254** **A**
S. globularia	/	/	/
S. invicta	**0.063±0.081** **B**	**0.054±0.046** **B**	**0.603±0.427** **A**

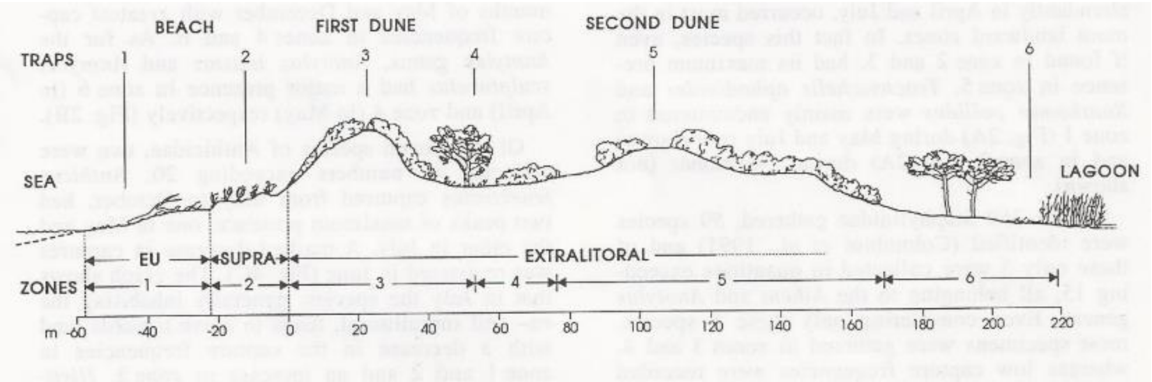


Figure 1.1: Diagram of the zones of a sandy beach-dune system from Fallaci, Colombini, and Chelazzi 1994

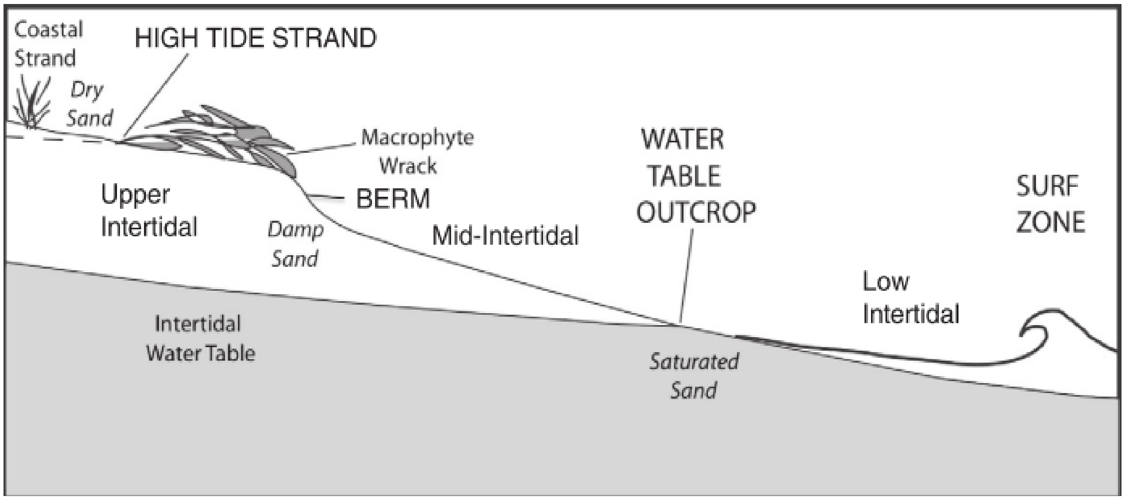


Figure 1.2 Diagram of the intertidal zone from Dugan et al. 2013

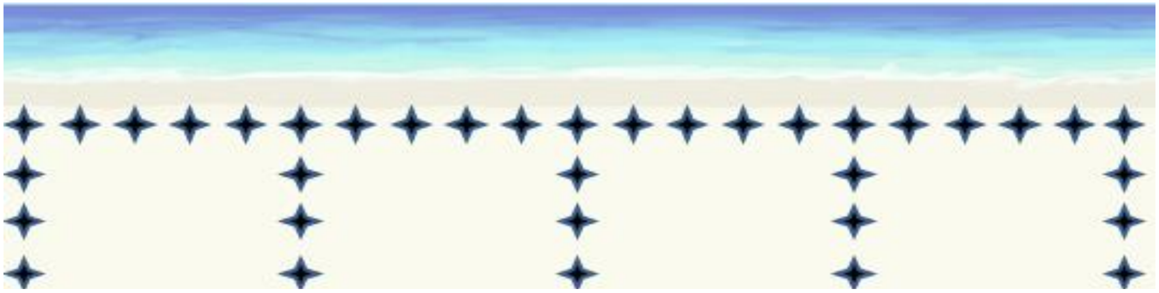


Figure 2.1: Plot design with each bait trap represented by a star. The front edge of the plot with 21 traps was positioned along the vegetation edge of the primary dune parallel to the shoreline. Five transects of three traps were placed perpendicular to the shoreline every 50 meters. Each trap was placed 10 meters from its nearest neighboring trap to form a 200 meter by 30 meter plot**.**

Figure 3.2: Reusable top loading bait trap showing the inner and outer sleeves which can be rotated into an open and

Figure 3.3: Plot design on left with each bait trap represented by a star. The front edge of the plot with 21 traps was positioned along the vegetation edge of the primary dune parallel to the shoreline. Five transects of three traps were placed perpendicular to the shoreline every 50 meters. Pictured at right is the dune vegetation edge on Sapelo, with a flagged trap at bottom center

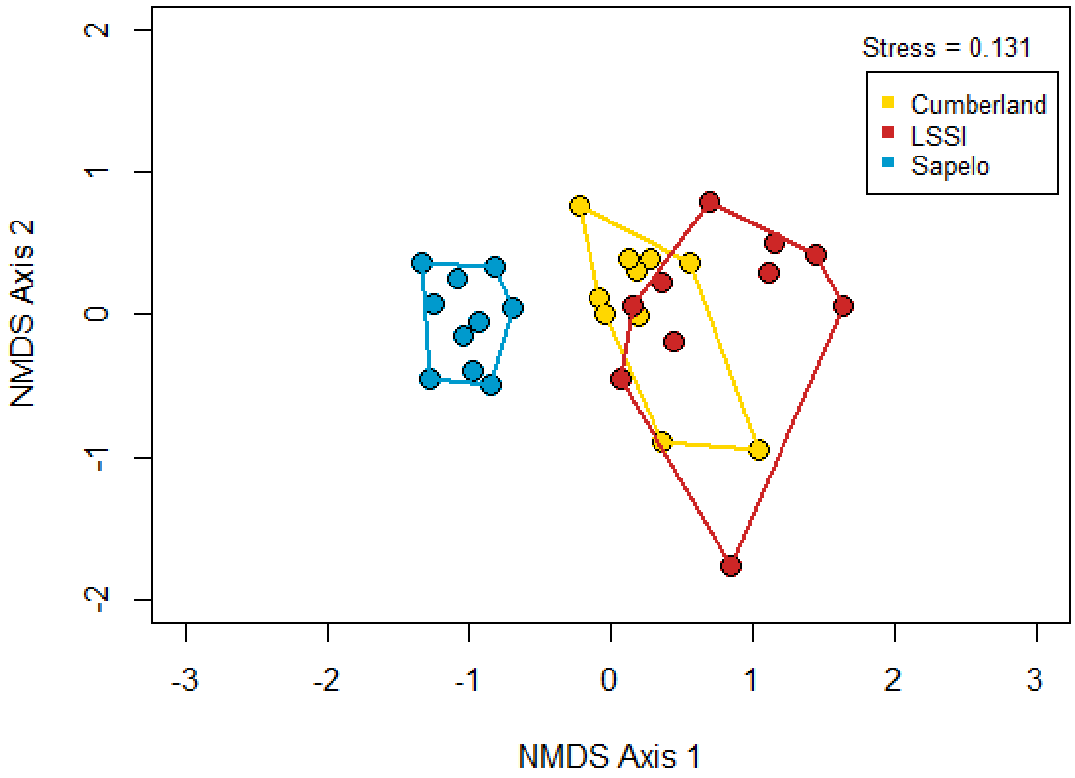


Figure 4.3: NMDS ordination using Bray-Curtis dissimilarity between the ant species assemblage of each plot surveyed. While there is overlap between the Cumberland and Little St. Simons clusters, there appears to be separation between each of the 3 islands indicating 3 dissimilar assemblages.

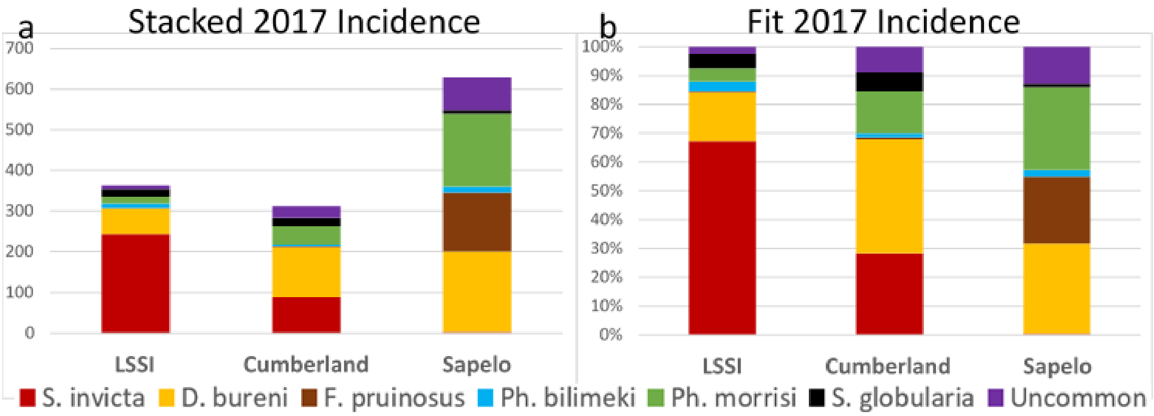


Figure 3.5: The community assemblage of each island for 2017. a) Stacked incidence count of each species collected on each island, with the 6 commonly encountered species noted and the remaining uncommonly encountered species pooled together. Sapelo has by far the highest amount of recruitment activity. b) The same incidence data as in plot a, but each island has had its assemblage fit to 100% so that the proportion of each species in each island's assemblage can be seen

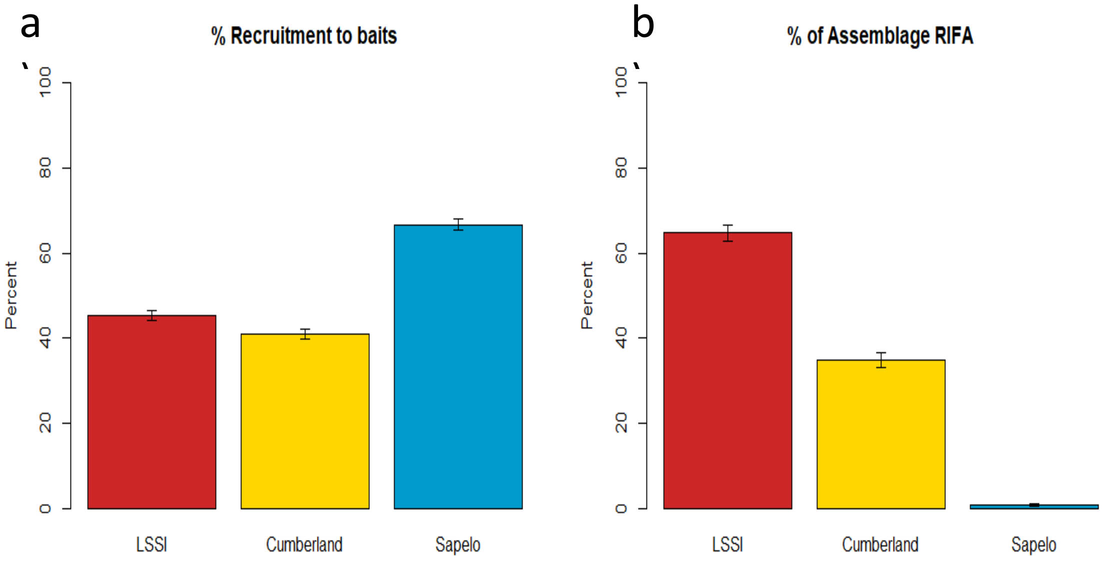


Figure 3.5: Recruitment of ants to baits. A is the proportion of traps that recruited ants for each island combining 2016 and 2017 surveys. B shows the proportions of S. invicta incidence in each island's ant assemblage for both years combined. Error bars are ± 1 standard error

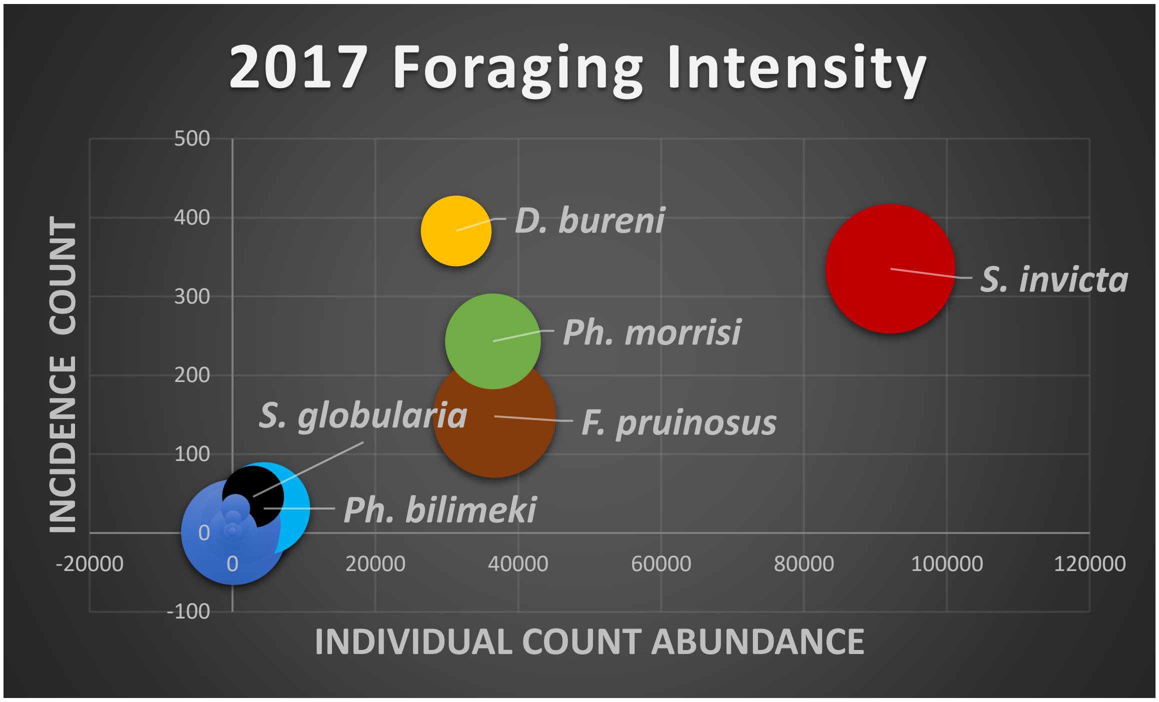


Figure 3.6: 2017 Foraging Intensity. Foraging intensity can be thought of as the number of individual ants (x-axis) encountered during each incidence (y-axis) of species presence. The size of each circle represents count abundance/incidence (x-axis/y-axis), with the size of the circle indicating the average intensity of a species' recruitment to a bait. The further a species is to the upper right, the more intensely it recruits to a food resource.

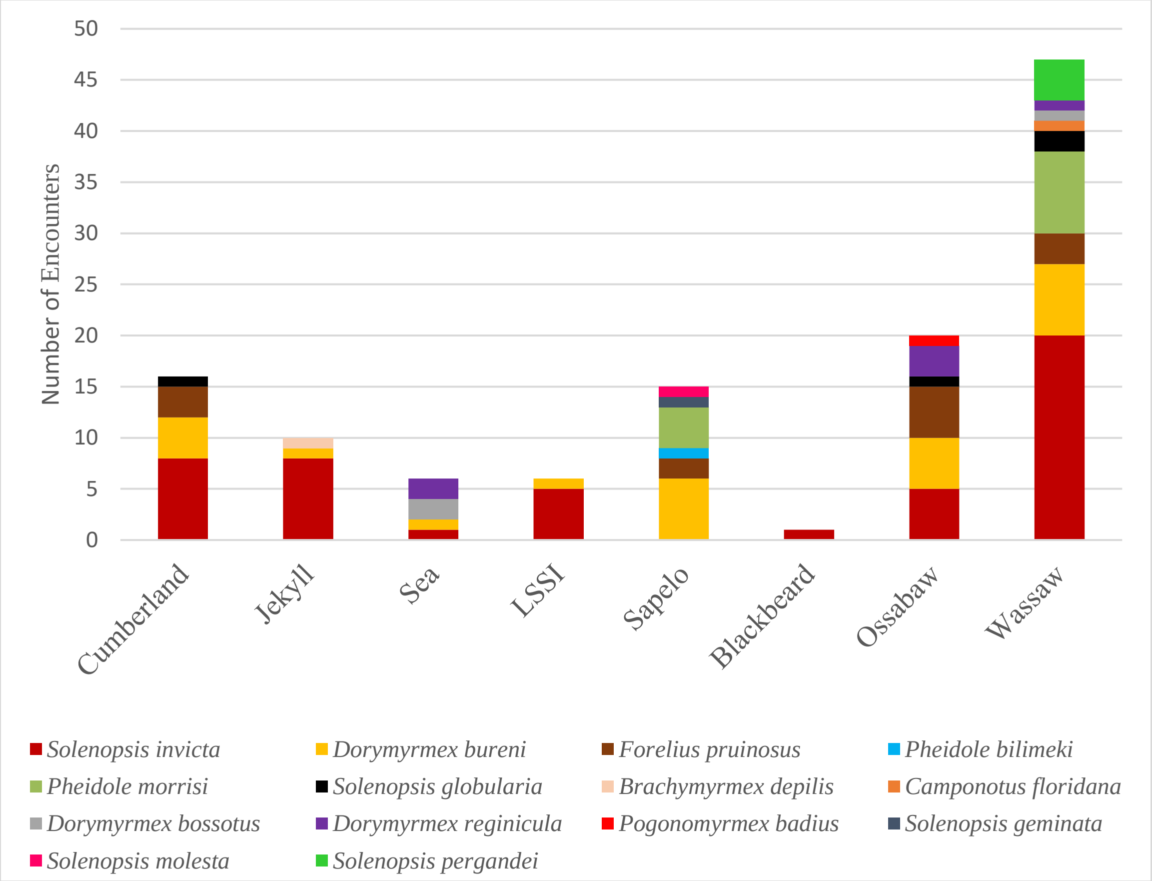


Figure 4.7: Ant species encountered at sea turtle nests by island along the Georgia coast

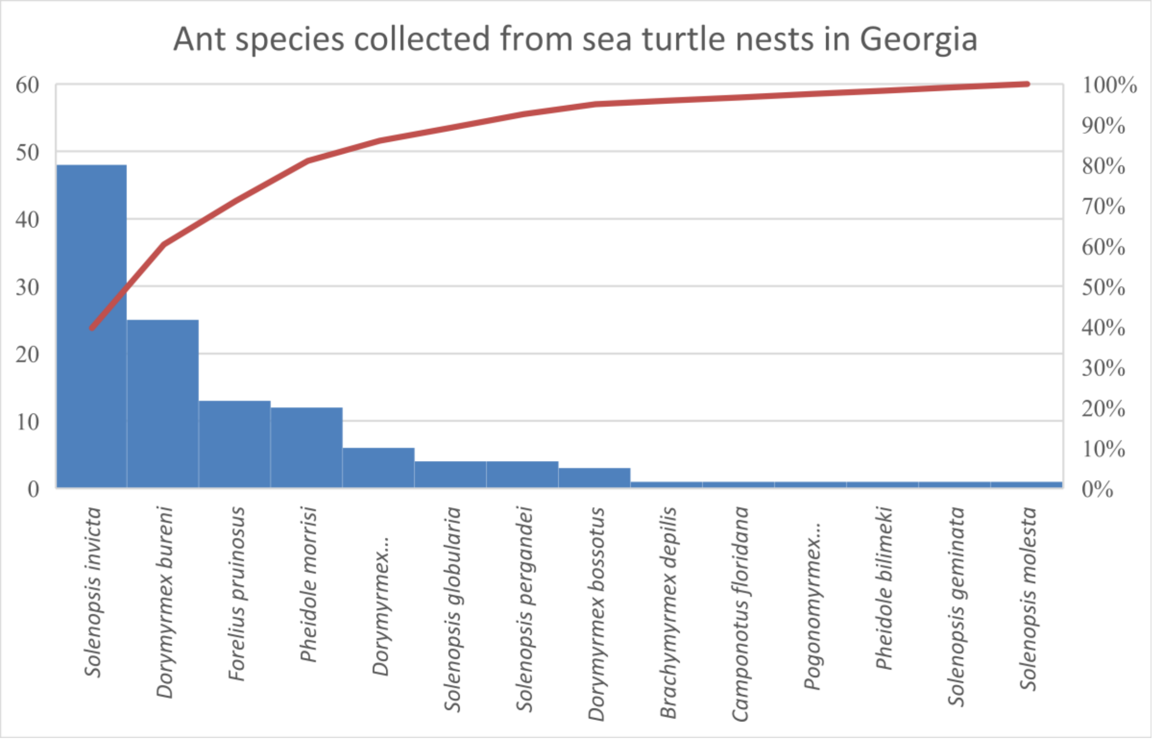


Figure 4.8: Ant species collected from sea turtle nests from all participating sea turtle projects along the Georgia coast. The line represents accumulation to 100%, shown on the right y axis.

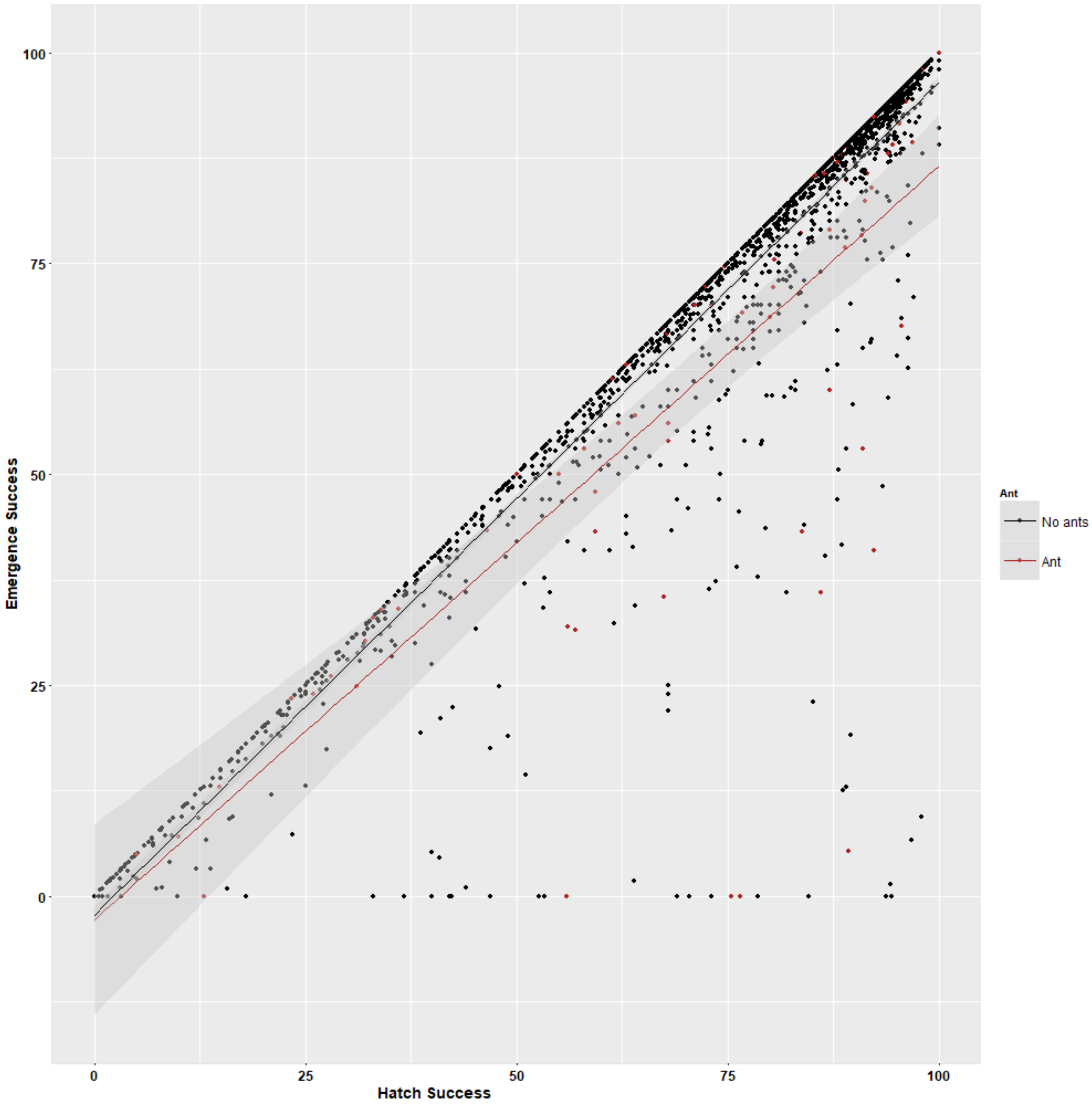


Figure 4.9: Regression analysis looking at the effect of ant presence **($R^2 = 0.618$, $p < 0.0001$)** or absence **($R^2 = 0.904$, $p < 0.0001$)** on sea turtle nest emergence success with nest hatch success as a covariate. The regression lines differ significantly once hatch success exceeds 50% with sea turtle nests with ants trending towards lower emergence success. Regression lines are plotted with 95% confidence intervals.