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CHARACTERIZING PATTERNS IN TEXAS GULF COAST BEACH DUNE PLANT SPECIES COMPOSITION

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CHARACTERIZING PATTERNS IN TEXAS GULF COAST BEACH DUNE PLANT
SPECIES COMPOSITION

By

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Presented to the Faculty of the Graduate School of

Stephen F. Austin State University

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ABSTRACT

Regional vegetation patterns of Texas beach plant communities were analyzed using cluster analysis, ANOSIM, SIMPER, NMDS, and ISA for five zones representing the foredune complex of twenty Gulf Coast beaches. ANOVA revealed that zones differ in terms of percent bare sand, percent vegetative cover, and species richness. Cluster Analysis, ANOSIM, and SIMPER results indicate that Texas beaches can be divided into northern and southern regions based on differences in species composition of plant communities. Indicator Species Analysis (ISA) indicates that northern beaches are characterized by the presence of *Rayjacksonia phyllocephala*, *Ambrosia Strophostyles*, *Ambrosia psilostachya*, and *Panicum amarum*. and southern beaches by the presence of *Ipomoea pes-caprae*.

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CHAPTER 1-LITERATURE REVIEW

Beach Systems

Sandy beaches are unique environments located on coastlines where terrestrial habitat meets marine habitat [15, 16]. Beach systems are subject to unique conditions, including wind, hydrology, and substrate [1, 6, 7, 8, 9, 15, 16] which shape the geomorphology of beaches and the composition of floral species found within them. Wind, hydrology, and substrate are elements of virtually all ecosystems, but in no other ecosystem do they work in tandem to create the same stressors and disturbances that can be found on coastal beaches [15, 16]. These stressors and disturbances form a gradient across the beach that creates multiple microhabitats [1, 2]. Between these microhabitats, the adaptive strategies needed to survive vary [2]. These microhabitats and their accompanying stress regimes shift with increasing distance away from the swash zone [1, 2]. The presence of microhabitats and the unique interactions between wind, hydrology, and substrate create a macrohabitat that is capable of accommodating a wide range of plant species that are each evolved for different environmental conditions [16].

Barrier Islands

Barrier islands are islands that form between a large body of water and the mainland of a larger landmass [13]. There are three proposed processes by which barrier islands can form over the course of thousands of years [13]. Dune drowning forms a barrier island when a rise in sea level cause a particularly highly elevated dune ridge to

become isolated and surrounded by water on all sides [13]. Spit accretion forms a barrier island when sand is continuously trapped by an extended portion of the mainland and that extension continues to grow outward away from the mainland until it has accrued enough sand to be a stand-alone island [13]. Shoal emergence forms a barrier island when an underwater sand bar grows from sand accumulation and eventually rises out of the water and above sea level [13].

Barrier islands can be classified as high-profile or low-profile [13]. High-profile barrier islands are characteristically wide, have a high elevation relative to sea level, and have healthy dunes with abundant vegetation [13]. Some examples of high-profile barrier islands along the Gulf Coast of the United States are Sanibel Island, Florida; Matagorda Island, Texas; and Padre Island National Seashore, Texas [13]. Low-profile barrier islands are characteristically narrow, have a low elevation relative to sea level, and exhibit fragmented dune systems very susceptible to erosion and overwash [13]. Some examples of low-profile barrier islands along the Gulf Coast of the United States are South Padre Island, Texas; Chandeleur Islands, Louisiana; Dauphin Island, Alabama; and St. George Island, Florida [13].

Coastal Dunes

Coastal sand dunes are created when wind coming inland from over the ocean shifts the sand into long mounds that extend the length of the shoreline [1, 16]. These dunes undergo an embryo dune stage before becoming foredunes [17]. The transition from embryo dune to foredune is facilitated by increasing sand accumulation. This sand

accumulation is made possible by the arrival of colonizer plant species that capture more sand with their vegetative parts [1, 17]. Numerous other dune types and dune system regions may arise depending on the particular region. Yellow dunes form further inland, behind the foredune, and exhibit different composition of substrate and more nutrients [18]. Grey dunes form even further inland than yellow dunes and exhibit increasing stability [18]. Plateaus and hollows are flat regions found between dune ridges and exhibit reduced levels of sand movement due to stabilization and plant colonization [1]. Blowouts are created when the vegetation of a dune is removed and sand is able to be shifted by the wind again, often resulting in a parabolic dune formation [7]. Humid and wet slacks are areas regularly exposed to a water source [7].

It is due to this variety of distinct dune system ecological zones that beaches are able to exhibit high levels of ecological diversity [16]. The biodiversity of each individual region increases further inland, i.e., regions such as the embryo dune or foredune will have lower biodiversity than the yellow dune or grey dune which are found farther away from the shoreline [16, 19]. This gradual rise in biodiversity is influenced by increases in richness and density. These increases occur due to stabilization of the habitat and reduction of disturbance and stress factors that constantly affect species that inhabit the regions closest to the ocean [2, 19].

Hydrology

Beach systems can be thought of as ecotones that separate the marine ecosystem of the adjacent sea from the terrestrial ecosystem found beyond the dunes [15]. Beach

systems are still drastically influenced by the hydrologic qualities of the ocean. Hydrology creates unique pressures that dune plants must be adapted for in order to survive [6]. Salinity and inundation are the two disturbance factors of marine hydrology that drive the species composition of a beach and its dunes [2, 4, 5, 6, 11, 20].

The high salt content of ocean water can easily damage plants that have been exposed to it unless the plants are adapted to either tolerate or avoid occasions of exposure. Salt tolerant plants are known as halophytes and have evolved numerous strategies for either combating or avoiding excessive salinity [5]. Specialized glands found in the tissues of various coastal plants such as *Sporobolus virginicus* (L.) Kunth have been shown to secrete excess levels of salt from their leaves and shoots [11, 21]. Other species, including *Cakile maritima* Scop. and *Kali turgidum* (Dumort.) Guterm., adapt to saline conditions by undergoing leaf hypertrophy when too many salt compounds have been absorbed [5, 23, 24]. The hypertrophy increases the leafy surface area of these plants by two or three times and helps in retaining water when Na^+ and Cl^- ions would otherwise impede water uptake [5, 11, 23]. Some halophytic species such as members of the genera *Atriplex*, *Chenopodium*, *Halimione*, and *Salsola* possess specialized hairs known as salt bladder trichomes [25]. Salt bladders exist as regular trichomes while also serving to store excess salt until they fill, mature, and abscise [25]. In addition to the aforementioned adaptations, halophytes may exhibit other adaptations including leaf abscission, salt exclusion methods, and reduced transpiration [5].

Many species that occupy the foredune do not possess any significant salt tolerance. These species often exhibit short life cycles so they can reproduce during the absences of adverse conditions [2, 5]. These short life cycles are often ended with the release of persistent seeds that are capable of surviving afloat or inundated for extended periods of time and are still able to germinate once favorable conditions return [2, 11, 12, 23]. Species such as *Ipomoea imperati* (Vahl) Griseb., *Sesuvium portulacastrum* (L.) L., and *Panicum repens* L. produce seeds that have been shown to germinate at high rates even after 40 days of uninterrupted exposure to saltwater [3]. The eventual germination of these persistent seedlings often occurs in the beginning of spring and is timed to coincide with the seasonal increase in precipitation that serves to decrease the salinity of the substrate [5]. Freshwater rinsing of seeds that were previously exposed to saltwater appears to be instrumental in the germination of many dune species. While many dune species can germinate in highly saline conditions, an even greater number will germinate after a subsequent exposure to freshwater [12]. In addition, a subsequent exposure to freshwater often allows the seeds of these plants to germinate after much longer periods of exposure to saltwater [12].

Sandy Substrate

The substrate of coastal beaches is made up of an enormous accumulation of sedimentary material [15]. These materials may be abiotic and originate from igneous rocks found in the ocean or they may be biotic and originate from coral, shellfish, or other marine organisms [15]. The exact textural and chemical composition of a beach's

sand is highly dependent on the local environment [15]. The substrate of beaches serves to form the dunes that the local flora will eventually colonize, but it also produces some of the primary stress factors that these plants will have to endure [4, 9, 10]. Sand is the coarsest soil type, and it is due to this large size that it can be particularly difficult for vegetation to grow in. Winds can potentially carry sand grains into vegetation at high enough velocities to impart mechanical damage [4, 10]. Sand is an excessively well-drained which makes it an extremely dry and nutrient-deficient substrate that plants must carry additional adaptations to survive [5]. The most important stress factor for dune plants to adapt to that pertains to sandy substrate is sand accretion [4, 5, 9, 23]. Sand accretion is the accumulation of sand at the base of plants through aeolian processes (movement via wind activity) that gradually buries them [10, 23].

The amount of sand that is moved by winds is extremely variable and highly reliant on an array of interconnected factors, namely the local region and its climate [10]. As the winds move sand grains, they will inevitably come into contact with vegetation growing on or around the dunes. Once a sand grain strikes a plant it will settle at that plant's base and become less affected by the wind's influence. After this occurs thousands of times the accumulating sand will eventually bury the plant unless the plant has adaptations for such a stress [9]. Steady increases in shoot growth are the most common and effective adaptation [9, 10]. Along the Gulf of Mexico, numerous dune species such as *Panicum amarum* Elliot, *Ipomoea pes-caprae* (L.) R. Br., *I. imperati*, and *Croton punctatus* Jacq. are all known to withstand sand accretion by increasing dry

biomass [10]. Populations of *Ammophila breviligulata* Fern. along the coast of Cape Cod have been shown to have a 72% positive correlation between weight in dry biomass and depth of sand burial [10]. Seeds and seedlings of dune species also carry specialized adaptations for dealing with sand accretion. Species including *Canavalia rosea* (Sw.) DC. And *Ipomoea pes-caprae* produce seeds capable of surviving and subsequently emerging from sand burial depths as deep as 16 cm [4]. Seeds of *Chamaecrista chamaecristoides* (Colladon) I. & B. have been shown to germinate and emerge from burial depths of 8 cm at a rate of 86% [4]. Studies attempting to explain what mechanism allows dune plants to respond to burial by increasing their growth rate have not yielded any conclusive answers [10]. Proposed answers claim that during burial plants may either contact mycorrhizal fungi that help them acquire more nutrients or escape from pathogens that are removed when fresh sand from the ocean replaces the previous sand [10]. Research seems to indicate that it is a combination of many factors, as well as a reactive growth response brought on by the sensation of burial, that promotes the growth of dune plants in response to burial by sand [10].

A lesser studied stress that sand can pose to dune vegetation is commonly known as sandblasting. Sandblasting occurs when sand grains become windborne and are carried into vegetation at a velocity capable of causing abrasions to the plant [4, 10, 26]. One study compared the effects of sandblasting on two inland species to a dune species found that dune species are adapted to such a stress [26]. When affected, sandblasting was found to inflict enough damage to reduce leaf area of the inland species, *Miscanthus*

sinensis Andersson and *Imperata cylindrica* (L.) P.Beauv., by up to 16% in some cases [26]. Furthermore, when salt spray was applied to the inland species immediately after sandblasting, reductions in leaf surface area of up to 81% were recorded [26].

Conversely, when the same treatments were applied to the dune species, *Carex kobomugi* Ohwi, there were no significant changes in leaf surface area at all [26]. This indicates that dune species possess unique adaptations for dealing with sandblasting that inland species do not possess [26]. It is speculated that dune species may be more tolerant of sandblasting due to a tougher cuticle, leaf morphology that inhibits direct collision with sand particles, or chemical adaptations that reduce the aggravating effects that subsequent salt spray can have on damaged leaves [26].

Sand as a substrate is excessively well-drained and it is this property of sand that makes sandy habitats very nutrient poor [5, 10, 23, 27]. Essential macronutrients such as nitrogen, potassium, and phosphorus are very seldom found at sufficient quantities in coastal dune systems so plants must develop methods of either accessing what is available or surviving with less [5, 23]. The dune species *Oenothera biennis* L. has adapted to lower quantities of N, P, and K by simply evolving to require less than the species found alongside of it [5]. The dune legume found along the Gulf of Mexico, *Strophostyles helvola* (L.) Elliot, has a symbiotic relationship with bacterial colonies that fix additional N for the plant [5]. The American beachgrass, *Ammophila breviligulata*, has formed a symbiotic relationship with vesicular-arbuscular-mycorrhizal (VAM) fungi that colonize its root system and improve its intake of phosphorus [5]. *Cakile maritima*

and *Kali turgidum* supplement their supplies of magnesium by absorbing it from salt spray [23]. *Atriplex prostrata* Bouchér ex DC. and *A. littoralis* L. absorb their magnesium from the sand itself [23]. Various species of *Cakile* have evolved to use Na rather than K in order to regulate their guard cells [23]. Certain species such as *Carex arenaria* L. and *Phleum arenarium* L. are able to translocate nutrients between their organs so ensure that nutrients are moved to wherever they are most needed [23]. Numerous other dune species possess additional adaptations for nutrient poor conditions including flexible root growth patterns that can target areas with higher a nutrient load, amplified propensity for interspecific or intraspecific competition over nutrients, or other ways of acquiring nutrients and requiring lower amounts of nutrients [23].

Water is the most vital nutrient that dune plants require but is often scarce in the dry and very effectively drained coastal dunes. Similar to the adaptation for sand accretion, an increase in growth rate can aid dune plants in finding sources of water [5]. The seedlings of *Ptelea trifoliata* L., *Lithospermum caroliniense* (Walter ex J.F. Gmel.) MacMill, *Calamovilfa longifolia* (Hook.) Scribn., and *Cakile edentula* (Bigelow) Hook. have been shown to have very high rates of vertical root extension when first sprouting in order to reach deep pockets of moisture within the sand [5]. Other dune species time their germination to coincide with the high precipitation of spring or the wet season and benefit in order to utilize all the water available when they need it most during adolescence [5]. Species such as *Cirsium vulgare* (Savi.) Ten. And *Cynoglossum officinale* L. grow successfully at much higher rates when underneath nurse plants which

shelter them from the heat, reducing their transpiration rates and preserving the water they acquire [5]. Other adaptations for water deficiency include succulent leaves that retain more water, CAM photosynthesis that reduces water loss during transpiration, and sheaths at the bases of seedlings or plants that shield the stem from excessive heat reflecting off of the sand [5, 23, 27].

Coastal Winds

Coastal winds are resultant of a pressure gradient that forms between the air above the land and the air above the ocean [15]. As the sun rises, the air above the land heats up and rises which causes the cooler air over the ocean to surge inland, creating a sea breeze [15]. At night, the air over the land cools more quickly than the air over the ocean. This process, known as a land breeze, works the same way as a sea breeze, only the pressure gradient is inverted [15]. The intensity and strength of these winds can possess enormous variance between locations based on factors such as geomorphology, flora, local climate, latitude, and infrastructure [15].

Wind is as important a factor in shaping beach environments as hydrology and substrate are [1, 8, 15, 16]. Coastal winds form the waves that crash into the swash zone and initiate the exchange of sediment between the ocean and the beach, known as littoral transport [15]. The wind regime of a beach will affect the wave types that will occur most often which will then affect aspects of nearby coastal currents, the structure of the beach, and the formation of the beach dunes [15].

Wind's most pertinent property as it influences dune plants is its role as the primary mover of sand [1]. When wind moves sand, the process can be called either erosion or deposition which are the displacement of sand from its position and the placement of sand in a new position, respectively [1]. Dune species can exhibit specialized tolerances to either one or both of these methods of sand movement [1]. *Croton punctatus* and *Palafoxia lindenii* A. Gray have been shown to dominate regions that exhibit higher rates of sand deposition [1]. *Chamaecrista chamaecristoides* has been shown to fair well in areas that experience high erosion rates as well as in areas with high deposition rates [1].

Dune Destruction

Coastal dunes exist as a natural barrier between the destructive force of storms and the inland environment [15, 16, 28, 29]. This function makes coastal dunes a particularly important structure, not only for the beach system as a whole, but also for any man-made structures located beyond them [28]. While dunes protect the interior ecosystem from storms, they are not themselves invulnerable [15, 28, 29]. The winds and waves generated by storms can annihilate dunes and the communities of plants inhabiting them [16, 28]. One such storm, affecting the dunes of Lake Huron, was extreme enough to eradicate entire populations of numerous annuals and biennials [16]. The removal of these dune species left a barren region that extended from the swash zone into the area that was previously the foredune [16]. Only after a month did sand begin to return to the barren foredune region and only after two years was the original community of *Cakile*

edentula, *Corispermum hyssopifolium* L., *Chamaesyce polygonifolia* (L.) Small, *Artemisia caudata* (Michx.) H.M. Hall & Clem, *A. breviligulata*, and *Calamovilfa longifolia* able to reestablish itself into the foredune again [16]. This example demonstrates that dune recovery after a storm can be quite prolonged. It should also raise concerns about how coastal systems and societies will handle the increasing frequency and severity of storms along coasts [30]. A study on St. George Island, Florida that modeled changes in dune vegetation alongside increased storm activity found that up to 63% of foredune species, 73% of interdune species, and 64% of backdune species will see declines in occurrence over the next 100 years [31]. An increase in storm activity was also shown to result in decreased species richness and diversity for every zone of a dune from the foredune to the backdune [31].

Wherein storm damage is a short-term cause of dune destruction, human impact is a long-term cause [32]. The human impact on a beach environment can be a contributing factor to the composition of the beach substrate, distribution and composition of the local plant and animal communities, morphology of the beach, and the overall health of the dunes [16]. The main purposes for human presence on beaches are agricultural, industrial, and recreational [16, 35]. A study quantifying the vulnerability of beaches along the Gulf Coast of Mexico found that only 19% of sites could be considered low vulnerability with the remaining 81% ranging from medium to high vulnerability [33]. In most cases these highly vulnerable sites experienced high levels of human disturbance due to tourism and the construction of infrastructure [33]. Another study looking at the

change in coastal dune area in Ravenna, Italy over the course of 60 years found that from the 1950's to the 1970's the development of housing reduced dune area by 72% [34]. By 1988 the amount of lost dune area was reduced to 61%, but as recently as 2011 only 25% of the original, pre-development dune system remains, meaning a roughly 75% loss in dune habitat since development began [34]. Some structures, including beach groins and seawalls, are built on beaches for the purpose of protecting human structures beyond the shoreline and, while they do serve that purpose for a time, they also further degrade the dune systems and may eventually become counterproductive to maintaining a healthy beach ecosystem [29]. Human impacts that ostensibly seem minor can have profound degrading effects on dunes. Intrusion upon dunes by individuals can unsettle the sand constituting a dune and stimulate erosion which can result in the loss of vegetation [29]. The loss of vegetation on a dune will promote further erosion and can initiate a positive feedback loop ultimately resulting in the complete degradation of the dune [29]. This process would be even more likely and more pronounced if the dunes were intruded upon by ATV's or other motorized vehicles [29].

Dune Preservation

Coastal dune systems are among some of the most damaged natural habitats by human activities [35]. Human settlements have often been drawn to bodies of water and this trend has not changed in the modern day [11, 15, 36]. Today there are 20 mega-cities, each with populations larger than 10 million people, within 60 km of a coastline [36]. These mega-cities plus the numerous other cities, towns, and villages found within

60 km of a coastline account for 40% of the world's population, and this value is expected to rise sharply in the coming years [35]. So much human settlement guarantees an accompanying human impact on the nearby ecosystems and an inevitable need to either reduce this impact or restore the ecosystems after damage to them has already occurred [35, 36, 37]. There are many methods of dune restoration and protection. Sand trapping mechanisms can be used to prevent the erosion of dunes before they can be properly colonized and stabilized by vegetation [29, 37]. Sand trapping is consistently used in conjunction with the transplantation of important plant species that will stabilize a dune [29, 37]. Transplants can be done with a range of colonial dune builders and will work best with local species [29, 37]. In 1992, sand trapping and a subsequent transplantation with *Ammophila arenaria* successfully restored a dune complex in Santander, Spain [37]. Dune transplantations can be supplemented with fertilizers which have been shown to increase seedling success in transplanted species by helping them to overcome the initial stress of nutrient deficiency [5, 29]. Occasionally a dune complex will need to be artificially reshaped [37]. Dunes are constantly growing from an embryo dune to a mature or fixed dune in a pattern of succession and changes in the local landscape or climate can influence a corresponding change in the dune's position [37]. In Cadiz, Spain, dune reshaping was used on a dune that began to move inland toward a pine plantation. The dune was reshaped, the shape was held together using fencing, and transplantation was implemented with the hope of stabilizing the dune in position [37]. Prevention is the most prudent, and sometimes the most effective, method of protecting

dunes. The public can be educated as to how to enjoy beach environments without damaging dunes by putting signs and informational bulletins in place [37]. The public can also be disinclined from participating in behavior that could damage dunes by putting up fencing around dunes, building walkover bridges, legally protecting dunes, enacting fines for damaging protected dunes, and erecting signs that advise beachgoers about the possible fines for damaging protected dunes [29, 37].

Beach nourishment, or the creation of artificial dunes, may be necessary when all other methods have been exhausted and the natural dunes of an area are either entirely gone or are unable to be restored by other means [29, 38]. The sand needed for artificial dune construction must be brought in from an outside source as relocating sand from a different section of the beach simply moves the problem [29]. The imported sand can have many dissimilarities with the local sand that may cause issues with dune stabilization and vegetation [15, 29, 38]. Factors including the size and coloration of the grains and the chemical properties of the grains must be accounted for before the imported sand can be used [15, 29, 38]. Once construction of the artificial dune begins, it must be as close as possible to the dimensions of the natural dune system that existed before it or still exists in fragments [29]. This will create a uniform, cohesive dune system more resistant to further degradation and erosion [29]. If these rules of thumb are not followed during beach nourishment it can result in the failure of the project and severe losses in time and money [15]. One such project intended to replenish the sand supply of Port Canaveral, Florida but failed when the imported grain size was too fine.

The end result was the loss of all of the imported sand by two years [15]. When performed properly, beach nourishment is an essential tool in restoring the beach environments that have damaged by human activity. Miami Beach, Florida implemented multiple dune restoration techniques in order to restore 15 kilometers of dunes along the beach [15]. Sand was dredged, tested to ensure it was fit for the local dune system, shaped into dunes using bulldozers, and transplanted with dune stabilizing colonizers [15]. Nearly 25 years after the project's completion the dunes were still stable and vegetated [15].

Floristic Studies on the Texas Gulf Coast

Studies focusing heavily on the composition and abundance of flora along the Texas Gulf Coast are rare. The areas that receive the most research attention are Padre Island and South Padre Island. The coastal vegetation belonging to the northern 1/3rd of North Padre Island was catalogued in a 1991 study that recorded the species observed as well as the beach region where they were found [45]. This study did not specify which portion of the dune the dune species inhabited and provides an incomplete assessment of the specific microhabitat that each species prefers. The vegetation of South Padre Island dunes has also been extensively catalogued [46, 47]. A 1977 study of South Padre Island recorded the dune species observed as well as whether they were located on the windward or leeward slope of the dune [47]. Another South Padre study from 2008 related coverage of dune vegetation to dune stability [46]. Any studies on the dunes of other Texas barrier islands are exceedingly hard to find and they typically fail to record

and incorporate plant community data into their findings. The single study spanning the entire Texas coastline was performed for the Texas General Land Office in 2009 [48]. However, this study only mapped the topography of the coastline and did not collect any plant community data [48]. The relative lack of studies that focus on plant communities along the Texas Gulf Coast leaves efforts such as dune rehabilitation, dune stabilization, and coastal community management without vital data that could greatly improve results.

CHAPTER 2-INTRODUCTION

The beach is a highly disturbed and stressful ecosystem presenting some unique challenges for the vascular plants that inhabit it. These disturbances can be attributed to the physical and hydrological properties of sand, the action of wind and waves, and the salinity of sea water [1, 6, 7, 8, 9]. Sand is a loose substrate that is constantly shifting due to wind [9, 10] and wave activity [44]. Shifting sands can affect beach plants by revealing the root systems or by burying plants [9, 10]. Beach plants must be adapted to extend root systems deeper into the sand or accelerate upward growth in order to avoid these problems [9, 10]. The hydrology of beach systems entails high salinity and the possibility of inundation. This requires beach plants to adapt in order to retain as much water as possible and avoid burial under constantly shifting sands [1, 5, 9, 10]. The saline water of beach systems creates a unique stress for plants to overcome [2, 6]. Given the fluctuations of waves and tidal forces, water can also completely inundate plants for lengths of time [4]. Plants may adapt to tolerate high salinity by secreting excess salt [11], storing salt in specialized hairs for later removal [25], or hypertrophy of leaves which will enlarge the leaves and dilute the salt-content [5, 23, 24]. Sand is the coarsest soil type and because of this it is very loose and is unable to efficiently hold nutrients or water [5]. Macronutrients and moisture drain through the sand particles before plants can absorb the quantities typically required for survival [5, 23]. Dune species must supplement their nutrient and water consumption by adapting to need less [23],

coevolving symbiotic relationships with organisms that can fix additional stores of nutrients for them [5], or adapting to absorb nutrients from unlikely sources such as salt spray [23] and the sand itself [23].

Environmental stresses increase towards the shoreline, creating a cline of microhabitats inhabited by differing communities of plants [1, 2] based on the beach zone [3]. The levels of disturbance and the types of stressors that affect each zone are highly indicative of which species will grow in which zone [3]. These regions include the swash zone, the foreshore, the berm, the dune, and the backdune. The swash zone receives the water of breaking waves as it runs up and then back down the beach and can be characterized as a region of intense disturbance and stress where no vegetation can grow due to perpetual inundation and constant shifting of substrate by waves [4]. The foreshore is demarked by the distance wave water reaches during high tide and like the swash zone is characterized by an absence of vegetation due to high disturbance levels [4, 44]. The berm experiences a reduction in disturbance activity and with adaptations for the stresses of nutrient unavailability and salinity certain plants can begin a vegetation line in this region [4]. The dune is a vegetated and elevated mound of sand. The front of the dune is subject to many of the same stressors as the berm and may be home to the same species that initiated the vegetation line [6, 7]. The crest of the dune will experience a further reduction in disturbance levels. The backdune is an ecotone of dune and inland environments located behind the dune [44]. In the backdune, competition

begins to replace disturbance tolerance as the primary adaptive strategy and shrubs or small trees not suited for the earlier regions will begin to appear [4, 44].

The 590 kilometer-long Gulf Coast of Texas runs southeast from Louisiana to Corpus Christi, and south from Corpus Christi to Mexico. The climate shifts in temperature and humidity from the higher latitudes to the lower latitudes. The southeastern region of Texas, from the border with Louisiana to south of Galveston, is a moderately humid region with abundant rainfall [13]. Corpus Christi and the surrounding region is slightly drier and exhibits about equal rates of precipitation and evaporation [13]. The climate from Corpus Christi south to Mexico is hot and arid, and evaporation heavily exceeds precipitation rates [13]. These changes in climatic regime may influence species composition along the Gulf Coast of Texas.

Despite the great length and climate shifts along the Texas Gulf Coast, there have been few floristic studies of the Texas beach communities [45, 46, 47, 48]. The objectives of this study are: 1) To characterize beach plant community types by zones along a transect from the vegetation line to the backdune along the entire Gulf Coast of Texas and identify indicator species for these zones; 2) to identify indicator species for regions of the Texas Coastline; 3) to examine the effect of human disturbance on Texas beach communities.

CHAPTER 3-MATERIALS & METHODS

Beach Selection and Disturbance

Twenty beach sites were sampled along the entire Texas Gulf Coast from Sea Rim in the northeast to South Padre Island in the southwest in October 2019 (**Fig. 1**). Sites were selected based on accessibility and included both publicly accessible beach sites and preserved sites in order to represent a range of human disturbance conditions. Measurements of beach structure were taken before dune sampling began including: dune length, dune height, the distance from the swash zone to the vegetation line, and the distance from the vegetation line to the beginning of the dune were recorded (**Table 5**). These measurements were taken for three separate dunes at each site.

Human disturbance was quantified on a scale of one to five dependent on the varying degrees and types of human activity at a site (**Table 2**). Five factors of human activity were included: human presence at the beach, the presence of litter within the dunes, vehicular access, residential infrastructure, and industrial infrastructure. Human presence was defined as the presence of 10 or more people on a site at the time of sampling. The presence of litter was defined as any instance of discarded human garbage being located within the dune system. Vehicular access was defined as the legal and literal ability to drive a motorized vehicle onto the beach. Residential infrastructure was defined as the presence of residential buildings (beach houses, condos, hotels, etc.) behind the sampled dune system. Industrial infrastructure was defined as the presence of

industrial facilities (plants, factories, power stations, etc.). Each factor was weighted equally, and a single point was awarded for each factor exhibited by a site.

After each site was given a disturbance score, the value was used to categorize each site as either low, medium, or high disturbance. Disturbance scores of 1–2 qualified the site as low disturbance, a score of 3 qualified the site as medium disturbance, and a score of 4–5 qualified the site as high disturbance. These categories were used to form distinct classes of disturbance that could more effectively detect patterns between sites that arose due to changes in disturbance levels.



Figure 1 Map of all 20 of the study sites examined during research. The markers in blue denote the northern sites and the markers in red denote the southern sites.

Table 1 Beach Site Labels and Corresponding Locations

Label	Location	GPS
01.SR	Sea Rim State Park, Jefferson County	29°40'27.2"N 94°02'32.1"W
02.MC	McFaddin National Wildlife Refuge, Jefferson County	29°39'58.4"N 94°04'31.5"W
03.BO	Bolivar Peninsula, Galveston County	29°28'05.6"N 94°35'46.8"W
04.BF	Bolivar Flats, Galveston County	29°23'13.1"N 94°43'13.5"W
05.JB	Jamaica Beach, Galveston County	29°08'43.4"N 95°01'52.7"W
06.KH	Kelly Hamby Nature Trail, Brazoria County	29°04'03.3"N 95°07'43.7"W
07.SS	Stahlman Park, Brazoria County	28°58'24.3"N 95°15'28.9"W
08.QU	Quintana Beach County Park, Brazoria County	28°55'35.3"N 95°18'48.4"W
09.SN	Northern Sargent Island, Matagorda County	28°47'29.1"N 95°34'23.0"W
10.SA	Southern Sargent Island, Matagorda County	28°45'50.0"N 95°37'39.6"W
11.MA	Matagorda Beach, Matagorda County	28°35'17.1"N 95°57'27.0"W
12.AB	Port Aransas Beach, Nueces County	27°47'16.8"N 97°05'19.1"W
13.MI	Mustang Island State Park, Nueces County	27°40'17.9"N 97°10'12.8"W
14.WC	Whitecap Beach, Nueces County	27°34'44.0"N 97°13'18.0"W
15.PD	Padre Island National Seashore, Kleberg County	27°25'44.8"N 97°17'44.1"W
16.PW	Northern South Padre Island, Cameron County	26°15'38.3"N 97°11'17.0"W
17.PP	South Padre Island Beach Access #6, Cameron County	26°12'29.0"N 97°10'41.7"W
18.PB	South Padre Island Beach Access #4, Cameron County	26°09'22.5"N 97°10'15.6"W
19.PS	Isla Blanca Beach, Cameron County	26°04'06.8"N 97°09'17.1"W
20.BC	Boca Chica Beach, Cameron County	25°59'42.7"N 97°09'01.3"W

Table 2 Beach Site Labels and Corresponding Disturbance Categorization

Label	Human Disturbance
01.SR	1 (Low)
02.MC	5 (High)
03.BO	5 (High)
04.BF	3 (Medium)
05.JB	2 (Low)
06.KH	1 (Low)
07.SS	3 (Medium)
08.QU	4 (High)
09.SN	1 (Low)
10.SA	3 (Medium)
11.MA	2 (Low)
12.AB	5 (High)
13.MI	3 (Medium)
14.WC	4 (High)
15.PD	2 (Low)
16.PW	1 (Low)
17.PP	3 (Medium)
18.PB	3 (Medium)
19.PS	4 (High)
20.BC	3 (Medium)

Data Sampling

Three transects were randomly laid perpendicularly at each beach, yielding 15 quadrats per beach and 300 quadrats total. GPS coordinates were recorded for each transect (**Table 1**). Transects were chosen randomly and adequately spaced so as to represent distinct portions of the beach. Five one-meter square quadrats were placed along each transect starting at the vegetation line. The second, third, and fourth quadrats were placed on top of the dune and sampled the windward slope, crest, and leeward slope zones of the dune, respectively. The fifth quadrat was placed at a distance of 20% the total dune length behind the dune in order to sample the backdune zone. No quadrats overlapped.

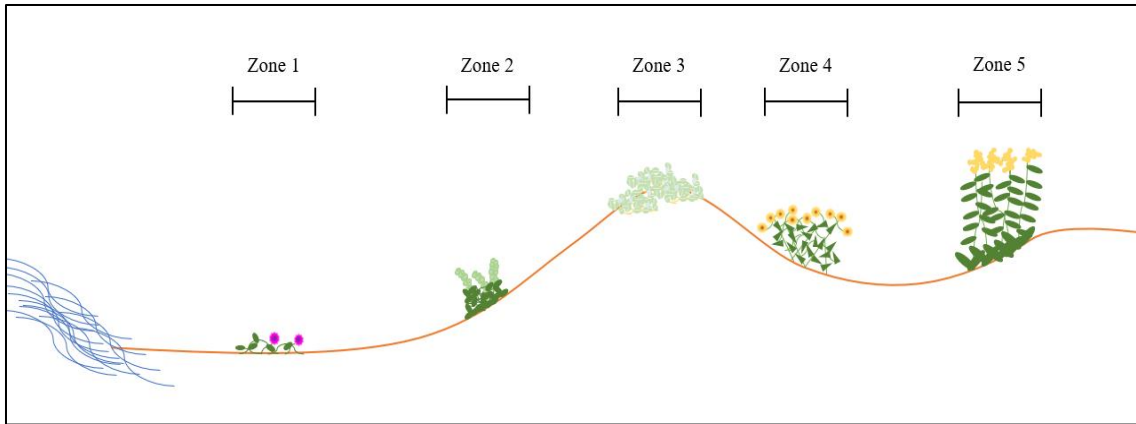


Figure 2 The five zones sampled and their approximate positions.

Each species located inside a quadrat was recorded. Many plants were given identifying designations and later identified *ex-situ*. Percent coverage per species was estimated using visual observations by dividing the quadrat into twenty-five 0.2 m² sections, each representing 4% of the total quadrat area. The percent coverage of each individual of a species was estimated by comparing each individual to the size of an 0.2 m² section. The estimated coverage of all individuals of a species was summed and recorded for each species within the quadrat. The percentage of decayed plant material that occupied the quadrat was also recorded in the same manner. Because individual could overlap each other within the plot, percent coverage could be higher 100%. The percent bare sand per quadrat was estimated following the same procedure.

Herbarium samples were taken from the first location where a species was observed and prepared for curation at the Stephen F. Austin State University herbarium (SFC). Some species could not be sampled because they occurred on beaches where destructive sampling was restricted. In these cases, *in situ* photographs were taken.

Forty-three species were identified in the study. Species data (presence/absence) were organized into Direct Gradient tables by zone and by beach. The Direct Gradient table for beach location was used to partition beaches into Northern (beaches 1–10) and Southern (beaches 11–20) regions (**Table 3**) as a factor in several analyses.

Table 3 Direct Gradient Table of Shifts in Species Occurrence along the Texas Gulf Coast

	SR	MC	BO	BF	JB	KH	SS	QU	SN	SA	MA	AB	MI	WC	PD	PW	PP	PB	PS	BC
<i>Schoenoplectus pungens</i>	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Paspalum vaginatum</i>	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cyperus esculentus</i>	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Vigna luteola</i>	8	2	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eclipta prostrata</i>	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ambrosia psilostachya</i>	7	-	1	4	-	6	8	7	6	8	6	-	-	-	4	-	-	-	-	-
<i>Rajacksonia phyllocephala</i>	3	1	-	8	9	1	6	3	2	6	-	-	-	-	-	-	-	-	-	-
<i>Aeschynomene indica</i>	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Strophostyles helvola</i>	3	1	-	1	9	3	8	11	4	-	-	-	-	-	-	-	-	-	-	-
<i>Heterotheca subaxillaris</i>	2	10	2	-	5	9	5	-	-	4	-	-	1	2	-	3	3	4	6	4
<i>Solidago sempervirens</i>	2	-	2	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sporobolus virginicus</i>	-	8	3	5	6	4	10	4	3	4	2	7	7	7	8	-	-	5	3	10
<i>Amaranthus greggii</i>	-	3	3	5	2	-	-	2	-	-	-	1	-	1	1	-	-	-	1	2
<i>Ipomoea imperati</i>	-	10	-	-	8	8	7	7	-	2	8	4	10	12	-	11	7	-	4	3
<i>Croton punctatus</i>	-	3	11	7	3	4	1	3	-	-	9	7	3	6	3	3	7	9	8	6
<i>Panicum amarum</i>	-	8	3	4	5	8	3	8	4	5	-	-	1	-	-	1	-	1	-	8
<i>Panicum repens</i>	-	3	-	3	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Oenothera drummondii</i>	-	-	1	-	-	3	-	-	5	3	-	-	3	6	7	3	-	-	-	1
<i>Helianthus praecox</i>	-	-	2	1	-	1	1	-	-	-	-	-	-	-	3	-	-	-	-	-
<i>Tamarix gallica</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sesbania drummondii</i>	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hydrocotyle bonariensis</i>	-	-	1	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Iva frutescens</i>	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sesuvium portulacastrum</i>	-	-	-	-	2	-	1	-	1	-	-	-	-	-	3	4	3	6	3	2
<i>Eragrostis secundiflora</i>	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cyperus strigosus</i>	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spartina patens</i>	-	-	-	-	-	5	-	1	8	5	-	-	-	2	2	-	-	-	-	-
<i>Symphotrichum subulatum</i>	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Paspalum monostachyum</i>	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chamaecrista fasciculata</i>	-	-	-	-	-	1	2	-	2	-	-	-	6	2	-	-	1	4	-	3
<i>Rubus trivialis</i>	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cyperus odoratus</i>	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-
<i>Physalis cinerascens</i>	-	-	-	-	-	-	-	-	2	2	-	-	-	-	-	-	-	2	5	1
<i>Aphanostephus skirrhobasis</i>	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
<i>Tidestromia lanuginosa</i>	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-
<i>Chamaesyce maculata</i>	-	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-	1	-	4
<i>Uniola paniculata</i>	-	-	-	-	-	-	-	-	-	-	8	-	-	2	-	7	4	-	-	-
<i>Ipomoea pes-caprae</i>	-	-	-	-	-	-	-	-	-	-	5	2	5	-	9	1	7	9	5	5
<i>Helianthus argophyllus</i>	-	-	-	-	-	-	-	-	-	-	3	6	-	4	-	-	-	-	-	-
<i>Heliotropium curassavicum</i>	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
<i>Conoclinium betonicifolium</i>	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
<i>Dactyloctenium aegyptium</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
<i>Schizachyrium littorale</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	3

All of the unique species recorded over the course of the study are displayed in the far-left column, and all sampled sites are displayed in the top row. The number in each cell indicates the number of times each species was seen in each site. Larger numbers resulted in darker shading which indicated increased sightings. A dash (-) signifies that the species was not present in the site listed in the top of the column. The sites progress from northernmost on the left to southernmost on the right.

Table 4 Direct Gradient Table of Shifts in Species Occurrence across Dune Zones

	1	2	3	4	5
<i>Ipomoea imperati</i>	24	23	21	17	10
<i>Sporobolus virginicus</i>	22	24	17	14	19
<i>Sesuvium portulacastrum</i>	15	8	1	-	1
<i>Croton punctatus</i>	11	23	26	20	7
<i>Ipomoea pes-caprae</i>	8	12	11	10	7
<i>Amaranthus greggii</i>	7	8	4	1	1
<i>Panicum amarum</i>	6	11	17	14	11
<i>Rajacksonia phyllocephala</i>	5	12	13	6	3
<i>Spartina patens</i>	3	6	2	5	7
<i>Schoenoplectus pungens</i>	3	3	3	3	2
<i>Paspalum vaginatum</i>	2	1	-	-	-
<i>Uniola paniculata</i>	1	3	6	4	7
<i>Tidestromia lanuginosa</i>	1	1	1	-	-
<i>Heliotropium curassavicum</i>	1	-	-	-	-
<i>Ambrosia psilostachya</i>	-	7	17	16	17
<i>Strophostyles helvola</i>	-	5	10	11	14
<i>Heterotheca subzillaris</i>	-	3	12	21	24
<i>Oenothera drummondii</i>	-	3	6	14	9
<i>Vigna luteola</i>	-	2	2	3	5
<i>Cyperus odoratus</i>	-	2	-	-	-
<i>Chamaecrista fasciculata</i>	-	1	5	5	10
<i>Helianthus argophyllus</i>	-	1	2	4	6
<i>Helianthus praecox</i>	-	1	1	4	2
<i>Schizachyrium littorale</i>	-	1	1	1	2
<i>Hydrocotyle bonariensis</i>	-	1	1	1	1
<i>Cyperus esculentus</i>	-	1	-	-	1
<i>Symphotrichum subulatum</i>	-	1	-	-	1
<i>Eclipta prostrata</i>	-	1	-	-	-
<i>Chamaesyce maculata</i>	-	-	3	3	2
<i>Physalis cinerascens</i>	-	-	1	5	6
<i>Panicum repens</i>	-	-	1	3	4
<i>Paspalum monostachyum</i>	-	-	-	1	1
<i>Aeschynomene indica</i>	-	-	-	1	-
<i>Conoclinium betonicifolium</i>	-	-	-	1	-
<i>Solidago sempervirens</i>	-	-	-	-	5
<i>Rubus trivialis</i>	-	-	-	-	2
<i>Tamarix gallica</i>	-	-	-	-	1
<i>Sesbania drummondii</i>	-	-	-	-	1
<i>Iva frutescens</i>	-	-	-	-	1
<i>Eragrostis secundiflora</i>	-	-	-	-	1
<i>Cyperus strigosus</i>	-	-	-	-	1
<i>Aphanostephus skirrhobasis</i>	-	-	-	-	1
<i>Dactyloctenium aegyptium</i>	-	-	-	-	1

All of the unique species recorded over the course of the study are displayed in the far-left column, and all sampled dune zones are displayed in the top row. The number in each cell indicates the number of times each species was seen in each dune zone. A dash (-) signifies that the species was not present in the dune zone listed in the top of the column.

Table 5 Mean Topographical Measurements of Each Beach Site

Label	Dune Length (m)	Dune Height (m)	Distance from Swash Zone to Vegetation Line (m)	Distance from Vegetation Line to Dune (m)
01.SR	7.33	0.30	32.40	2.23
02.MC	9.07	0.90	31.20	4.90
03.BO	6.30	0.70	38.07	0.00
04.BF	7.60	0.90	41.83	2.37
05.JB	7.00	1.30	26.67	3.13
06.KH	8.67	0.90	27.57	0.57
07.SS	8.70	1.10	16.37	1.30
08.QU	8.07	1.53	23.47	0.67
09.SN	6.60	0.90	10.07	1.90
10.SA	5.47	1.20	9.27	0.33
11.MA	43.60	2.80	73.87	1.80
12.AB	32.03	6.00	61.50	2.43
13.MI	9.20	1.10	20.60	0.00
14.WC	28.47	6.00	14.73	0.00
15.PD	10.73	1.40	15.60	0.33
16.PW	17.20	5.00	40.17	0.17
17.PP	7.80	1.20	0.00	0.00
18.PB	9.10	1.20	0.00	0.00
19.PS	25.80	1.20	13.13	1.30
20.BC	7.33	1.20	12.40	0.00

Species Richness (S), Shannon's Diversity (H'), and Pielou's Evenness (J')

Species richness was used as a measure of biodiversity and as a variable used to calculate evenness. Richness was recorded as the count of all species found within a specific range of data, e.g., species seen in a site or in a dune zone.

The diversity of plant communities was calculated using Shannon's diversity equation:

$$H' = -\sum p_i \ln p_i$$

p_i is the fraction of the percent coverage of individuals of species i within the population. p_i was calculated by dividing the percent coverage of species i within each quadrat by the total percent coverage of all species within the quadrat. Shannon's Diversity Index was calculated separately for beach zones and by beach location. The use of percent coverage in Shannon's as a replacement for abundance is noted in other such studies that document plant life on beach dunes [63] or coral biodiversity [22].

Shannon's diversity can be difficult to interpret as it can provide a wide range of values. In order to standardize the resulting Shannon's Diversity values on a 0 to 1 scale, Pielou's evenness was calculated:

$$J' = H' / \ln (S)$$

The diversity and evenness values were calculated in multiple ways. Diversity and evenness were calculated for dune zones across all sites (**Table 6**), for each site (**Table 7**), for each dune zone within each beach site (**Table 8**), and for each of the three replicate transects for each site (**Table 9**).

ANOVA

Analysis of variance (ANOVA) testing was performed using SAS[®] software [49]. ANOVA was used to analyze the potential influences that site, dune zone, and disturbance have on dependent environmental variables such as species richness, percent of sandy cover, and percent of vegetative cover. Every ANOVA was performed with an alpha value of 0.05. The model for the ANOVA was as follows:

$$Y_{ijkl} = \mu + D_i + S_{j(i)} + R_{(ij)k} + Z_l + \varepsilon_{ijkl}$$

μ represents the overall mean value of the dependent variable. Y represents the dependent variable. D represents the fixed disturbance effect. S represents the random site effect. R represents the random effect of replicates. Z represents the fixed dune zone effect. ε represents the random error in the model. This model was applied three times using species richness, percent bare sand, and percent vegetative cover as dependent variables. Q-Q plots of each dependent variable indicated that the data were normally distributed. Tukey's pairwise comparison was used on each significant effect in order to identify which comparisons were significant.

Cluster Analysis

Agglomerative hierarchical clustering was used to group sites based on similarities of species composition using the flexible beta method in order to grant more freedom in analyzing the data. A community data matrix of species abundances was transformed into a Sorensen distance matrix in R using the labdsv package [39, 74]. Flexible beta agglomerative hierarchical clustering was performed on Sorensen distances in R using the cluster package [39, 73]. The alpha value was set to 0.625 and the beta value was set to -0.25.

ANOSIM, SIMPER, and NMDS

Analysis of similarities (ANOSIM) and similarity percentage (SIMPER) were used to analyze differences in species abundances based on beach zones and region [39, 41]. ANOSIM and SIMPER utilize a community data matrix of species abundance to identify whether or not there are significant differences between or within groups of data and can be used with non-parametric data. ANOSIM uses Bray-Curtis dissimilarity in order to assign dissimilarity rankings to each group and compare the average dissimilarity ranks between groups to the average dissimilarity ranks within groups. ANOSIM produces an R-value and a significance value to identify any significant differences within or between groupings. The R value ranges from -1 to 1. A value close to 1 indicates high levels of dissimilarity between groups, a value close to 0 indicates roughly equal amounts of dissimilarity between groups and within groups, and a value under 0 indicates high levels of dissimilarity within groups. SIMPER produces pairwise

comparisons of every site or zone combination and provides an ordered list of the species that contributed to the dissimilarity between the sites the most.

ANOSIM and SIMPER tests were performed on abundance data using the vegan package in R [39, 41]. Dune zones and geographic location of beaches were used as vectors and were run separately. ANOSIM and SIMPER for dune zones were performed using a community data matrix of species abundance by dune zone. The five different dune zones were used as a vector with an alpha value of 0.05. ANOSIM and SIMPER for beach sites were performed three times using a community data matrix of species abundance by sample site. Beach location was used as a vector with an alpha value of 0.05. In the first analysis, the twenty sites were treated independently, and no groupings were made. The subsequent SIMPER analysis then analyzed the pairwise comparisons of each beach site as well as which species contributed most to dissimilarities between beach sites. ANOSIM and SIMPER were run a second time to test for regional patterns in the data set based on results of the flexible beta hierarchical agglomerative clustering analysis. Based on flexible beta results the beaches were divided into two regions, a Northern group consisting of ten beaches from Sea Rim (1) on the Louisiana border to the Sargent Island sites (9 and 10), and a Southern group of all sites from Matagorda Island (11) to Boca Chica State Park (20) near the Mexico border. ANOSIM and SIMPER were run a third time placing the Padre Island National Seashore (PD), a geographically southern beach, in the northern group as suggested by the flexible beta cluster analysis.

Non-metric multidimensional scaling (NMDS) was performed on a community data matrix of species abundances using the `ecodist` and `ggplot2` packages in R [39, 42, 43] to visualize patterns of similarity based on species abundances. Conditionality (K) for NMDS was maintained at two dimensions. This allowed for the least amount of stress on the NMDS results. NMDS was run twice, once by beach zones and once by beach location. NMDS of beach zones used percent sandy cover, species richness, and Pielou's evenness as interpretive environmental vectors. NMDS of beach location used latitude, longitude, percent sandy cover, total disturbance, dune length, and dune height as interpretive environmental vectors.

Indicator Species Analysis

Indicator species analyses (ISA) were performed using the `indicspecies` package of R [39, 40]. These analyses used dune zones, geographic location, and disturbance categories of the beaches as vectors. Analyses were run separately. ISA utilizes a community data matrix of species abundance in order to assign species as indicators of groupings. ISA provides informative values such as the specificity, fidelity, and `IndVal`. Specificity indicates the proportion of sites in a group occupied by a species relative to the total number of occurrences of that species across all sites [56]. Fidelity is the probability that the species will be found in sites belonging to the assigned grouping [56]. The indicator value, `IndVal`, is the square root of the product of the specificity and fidelity scores and indicates the strength of the relationship between the species and the assigned grouping.

For the dune zone ISA, a community data matrix of species by dune zone was analyzed in R using the *indicspecies* package [39, 40]. This ISA used dune zones 1 through 5 as a vector with an alpha value of 0.05. Zone 1 represented the vegetation line, zone 5 represented the backdune, and zones 2–4 were located sequentially between zones 1 and 5. R was allowed to test for indicator species for individual zones, as well as for combinations of zones.

For the regional ISA, a community data matrix of species abundance for each site was analyzed in R using the *indicspecies* package [39, 40]. The sites were categorized into northern or southern groupings based on a Direct Gradient table arrangement (**Table 3**) of species presence throughout all sites and cluster analysis results (**Fig. 4**). The northern grouping contained 10 sites that ranged geographically from the Texas border with Louisiana to Matagorda. The southern grouping contained 10 sites that ranged geographically from Corpus Christi Bay to South Padre Island and the Texas border with Mexico. The community data matrix was analyzed in R using the *indicspecies* package [39, 40] using regional groupings as a vector with an alpha value of 0.05.

For the disturbance level ISA, a community data matrix of species by site was analyzed in R using the *indicspecies* package [39, 40]. This ISA used sites classified into their respective disturbance level of either low, medium, or high, as vectors.

CHAPTER 4-RESULTS

Species Richness, Diversity, & Evenness

Species richness varied from a high of 11 species in zones 3 and 5 of the Kelly Hamby (KH) site and a low of two species in zone 1 of the Sea Rim (SR), Bolivar Peninsula (BO), and Northern South Padre Island (PW) sites. The average species richness varied between zones (**Table 6**) and by beach (**Table 7**).

In zones, percent sandy cover was highest in zone 1 at an average of 75.3% and lowest in zone 5 with an average of 6% (**Table 7**). Average percent sandy cover in sites varied from a high of 52% in McFaddin (MC) to a low of 9.69% in the Bolivar Peninsula site (BO) (**Table 8**). In zones, vegetative cover was highest in zone 5 at an average of 100.82% and lowest in zone 1 with an average of 26.88% (**Table 7**). Average vegetative cover in sites varied from a high of 96.13% in the Bolivar Peninsula site (BO) to a low of 49.37% in Bolivar Flats (BF) (**Table 7**). The calculations for Shannon's diversity and Pielou's evenness in the different zones of each site were recorded in **Table 8**. The calculations for Shannon's diversity and Pielou's evenness for each site as a whole were recorded in **Table 9**.

Table 6 Overall Species Coverage and Density Values for Dune Zones

Zone	Sand	Coverage	S	H'	J'
1	75.32	26.88	14	2.199	0.833
2	35.45	68.50	27	2.371	0.719
3	23.12	79.83	25	2.660	0.798
4	13.15	91.07	26	2.805	0.842
5	6.00	100.82	36	2.920	0.797

Sand is the average percent coverage of sand that occupied each zone. **Coverage** is the average percent coverage of vegetation that occupied each zone. **S** represents the species richness for a zone. **H'** and **J'** are the average Shannon's Diversity and Pielou's evenness values, respectively, for each zone.

Table 7 Overall Species Coverage and Density Values for Sites

Zone	Sand	Coverage	S	H'	J'
SR	34.73	70.29	11	1.453	0.567
MC	52.00	53.63	10	1.754	0.762
BO	9.69	96.13	12	1.666	0.670
BF	48.87	49.37	11	1.513	0.631
JB	34.40	77.03	12	2.072	0.834
KH	38.00	70.83	15	2.311	0.853
SS	30.87	81.83	13	2.064	0.805
QU	21.80	92.82	9	1.557	0.709
SN	28.00	62.14	13	1.959	0.742
SA	15.00	84.75	11	1.931	0.753
MA	26.00	84.01	9	1.805	0.822
AB	35.93	63.27	6	1.064	0.594
MI	21.40	77.33	10	1.871	0.780
WC	26.47	79.60	10	2.016	0.876
PD	25.13	77.87	10	2.005	0.871
PW	35.00	67.21	9	1.701	0.774
PP	39.47	62.74	7	1.749	0.899
PB	34.00	68.36	9	1.816	0.827
PS	29.47	73.33	8	1.588	0.764
BC	25.93	75.81	13	2.272	0.886

Sand is the average percent coverage of sand that occupied each site. **Coverage** is the average percent coverage of vegetation that occupied each site. **S** represents the species richness for a site. **H'** and **J'** are the average Shannon's Diversity and Pielou's evenness values, respectively, for each site.

Table 8 Shannon's Diversity and Pielou's Evenness Values for the Dune Zones of Each Site

Site/Zone	H'	J'	Site/Zone	H'	J'
SR Z1	0.686	0.990	KH Z1	1.376	0.992
SR Z2	0.286	0.159	KH Z2	1.592	0.765
SR Z3	0.536	0.333	KH Z3	2.021	0.843
SR Z4	1.026	0.573	KH Z4	1.946	0.845
SR Z5	1.837	0.944	KH Z5	2.019	0.842
MC Z1	0.914	0.832	SS Z1	1.092	0.787
MC Z2	1.404	0.721	SS Z2	1.621	0.905
MC Z3	1.035	0.643	SS Z3	1.440	0.740
MC Z4	1.345	0.751	SS Z4	1.408	0.677
MC Z5	1.387	0.713	SS Z5	1.497	0.681
BO Z1	0.457	0.660	QU Z1	1.428	0.797
BO Z2	0.936	0.581	QU Z2	1.821	0.829
BO Z3	0.236	0.170	QU Z3	0.622	0.347
BO Z4	1.123	0.810	QU Z4	0.637	0.580
BO Z5	1.253	0.778	QU Z5	1.048	0.954
BF Z1	1.073	0.977	SN Z1	1.227	0.763
BF Z2	0.902	0.561	SN Z2	0.970	0.542
BF Z3	0.962	0.537	SN Z3	1.313	0.733
BF Z4	1.302	0.626	SN Z4	1.365	0.762
BF Z5	0.518	0.322	SN Z5	1.820	0.790
JB Z1	0.816	0.743	SA Z1	1.727	0.964
JB Z2	1.658	0.797	SA Z2	1.508	0.775
JB Z3	1.576	0.810	SA Z3	1.151	0.591
JB Z4	1.549	0.796	SA Z4	1.518	0.730
JB Z5	0.971	0.499	SA Z5	1.267	0.651

Table 8 (Continued)

Site/Zone	H'	J'	Site/Zone	H'	J'
MA Z1	0.888	0.808	PW Z1	0.512	0.738
MA Z2	0.896	0.646	PW Z2	1.440	0.895
MA Z3	1.415	0.727	PW Z3	1.423	0.884
MA Z4	1.092	0.561	PW Z4	1.508	0.937
MA Z5	1.333	0.744	PW Z5	0.957	0.534
AB Z1	1.175	0.848	PP Z1	0.933	0.673
AB Z2	0.654	0.472	PP Z2	1.124	0.811
AB Z3	1.071	0.975	PP Z3	0.838	0.605
AB Z4	0.000	N/A	PP Z4	1.249	0.776
AB Z5	0.000	N/A	PP Z5	1.422	0.883
MI Z1	0.968	0.881	PB Z1	1.113	0.803
MI Z2	0.934	0.580	PB Z2	1.307	0.943
MI Z3	1.277	0.793	PB Z3	1.413	0.789
MI Z4	1.312	0.674	PB Z4	1.483	0.922
MI Z5	1.658	0.852	PB Z5	0.860	0.442
WC Z1	0.652	0.593	PS Z1	0.779	0.562
WC Z2	1.380	0.858	PS Z2	0.710	0.512
WC Z3	1.381	0.771	PS Z3	0.672	0.612
WC Z4	1.419	0.792	PS Z4	0.753	0.468
WC Z5	1.554	0.747	PS Z5	1.062	0.766
PD Z1	0.708	0.644	BC Z1	1.142	0.824
PD Z2	1.555	0.966	BC Z2	1.910	0.919
PD Z3	1.722	0.961	BC Z3	1.784	0.812
PD Z4	1.628	0.908	BC Z4	1.797	0.780
PD Z5	1.460	0.665	BC Z5	1.795	0.817

Table 9 Shannon's Diversity and Pielou's Evenness Values for the Replicates of Each Site

Site/ Zone	H'	J'	Site/ Zone	H'	J'	Site/ Zone	H'	J'
SR	0.844	0.434	QU	1.356	0.652	PD	1.702	0.775
SR	1.465	0.667	QU	1.194	0.742	PD	1.475	0.823
SR	1.302	0.626	QU	1.152	0.643	PD	1.486	0.923
MC	1.293	0.721	SN	1.130	0.580	PW	1.382	0.859
MC	1.688	0.812	SN	1.831	0.795	PW	0.709	0.512
MC	1.218	0.626	SN	1.227	0.685	PW	1.435	0.738
BO	1.890	0.909	SA	1.415	0.727	PP	0.878	0.634
BO	0.948	0.684	SA	0.939	0.583	PP	1.294	0.804
BO	1.268	0.708	SA	1.226	0.684	PP	1.533	0.788
BF	1.336	0.687	MA	1.492	0.767	PB	1.112	0.691
BF	0.988	0.508	MA	1.674	0.860	PB	0.927	0.476
BF	0.891	0.458	MA	1.634	0.786	PB	1.745	0.974
JB	1.675	0.762	AB	1.093	0.788	PS	1.539	0.859
JB	1.256	0.645	AB	1.035	0.578	PS	1.231	0.633
JB	1.547	0.744	AB	0.938	0.677	PS	1.466	0.818
KH	1.753	0.798	MI	1.151	0.715	BC	1.600	0.822
KH	1.780	0.773	MI	1.569	0.806	BC	1.565	0.804
KH	1.625	0.835	MI	1.094	0.680	BC	1.618	0.903
SS	1.667	0.857	WC	1.557	0.800			
SS	1.913	0.798	WC	1.836	0.836			
SS	1.478	0.642	WC	1.159	0.720			

ANOVA

Species Richness

The model found that the interaction of dune zone and human disturbance had a significant influence on species richness ($p = 0.0171$) (**Table 10**). Since the interaction effect was significant the individual effects of human disturbance and dune zone were not relevant.

Table 10 Effects of Human Disturbance and Dune Zone on Species Richness (ANOVA)
Dependent Variable: Species Richness

Effect	Num DF	Den DF	F Value	p-value
Human Disturbance	4	15	0.90	0.4882
Dune Zone	4	220	6.88	<0.0001
Human Disturbance*Dune Zone	16	220	1.96	0.0171

Tukey's pairwise comparison was performed for the interaction between dune zone and human disturbance yielding 300 different comparisons, 52 of which were statistically significant. Because the effect of zones cannot be distinguished from disturbance we examined only the Tukey's comparisons of differing disturbance classes within the same zone (**Fig. 3**).

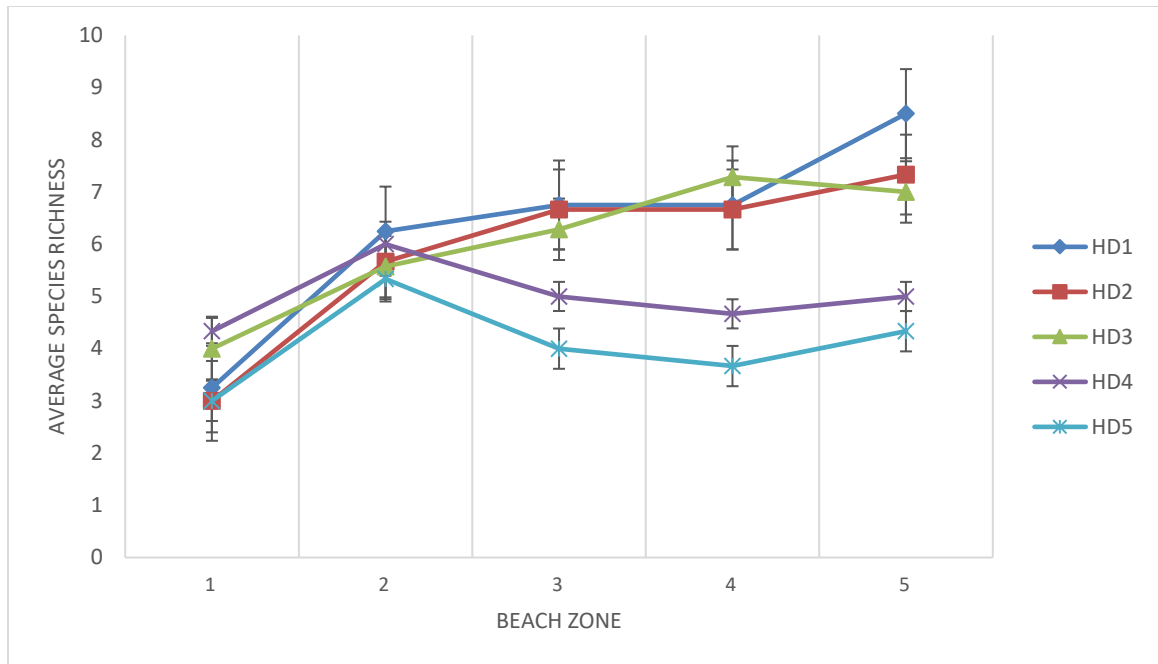


Figure 3 Changing Species Richness in Dune Zones by Human Disturbance Level

Percent Sand

The model found that that dune zone’s influence on percent sand was significant ($p = <0.0001$) (**Table 11**). Human disturbance alone and the interaction of dune zone and human disturbance did not significantly influence percent sand.

Table 11 Effects of Human Disturbance and Dune Zone on Percent Sand (ANOVA)
Dependent Variable: Percent Sand

Effect	Num DF	Den DF	F Value	p-value
Human Disturbance	4	15	0.28	0.8878
Dune Zone	4	220	86.68	<0.0001
Human Disturbance*Dune Zone	16	220	1.06	0.3995

Dune zone's influence on percent sand was significant so a Tukey's test was performed in order to identify which zones were significantly different from one another (**Table 12**). Every dune zone was significantly different from one another in percent of sand.

Table 12 Tukey's Pairwise Comparison of Zone's Effect on Percent Sand
Dependent Variable: Percent Sand

Zone	Zone	T Value	p-value
1	2	9.46	<0.0001
1	3	12.44	<0.0001
1	4	14.80	<0.0001
1	5	16.82	<0.0001
2	3	2.98	0.0032
2	4	5.34	<0.0001
2	5	7.36	<0.0001
3	4	2.36	0.0191
3	5	4.38	<0.0001
4	5	2.02	0.0443

Percent Vegetative Cover

The model found that that dune zone's influence on percent vegetative cover was significant ($p = <0.0001$) (**Table 13**). Human disturbance alone and the interaction of dune zone and human disturbance did not significantly influence percent vegetative cover.

Table 13 Effects of Human Disturbance and Dune Zone on Percent Vegetative Cover (ANOVA)

Dependent Variable: Percent Vegetative Cover				
Effect	Num DF	Den DF	F Value	p-value
Human Disturbance	4	15	0.88	0.4987
Dune Zone	4	220	62.20	<0.0001
Human Disturbance*Dune Zone	16	220	1.26	0.2264

Dune zone's influence on percent vegetative cover was significant so a Tukey's test was performed in order to identify which zones were significantly different from one another (**Table 14**). Dune zones 3 and 4 were the only zones to not be significantly different from one another in percent of vegetative cover.

Table 14 Tukey's Pairwise Comparison of Zone's Effect on Percent Vegetative Cover
Dependent Variable: Percent Vegetative Cover

Zone	Zone	T Value	p-value
1	2	-7.89	<0.0001
1	3	-10.01	<0.0001
1	4	-11.96	<0.0001
1	5	-14.69	<0.0001
2	3	-2.11	0.0356
2	4	-4.07	<0.0001
2	5	-6.80	<0.0001
3	4	-1.96	0.0516
3	5	-4.69	<0.0001
4	5	-2.73	0.0069

Cluster Analysis

Agglomerative hierarchical clustering of the site data produced a cluster tree containing all 20 sites. The tree breaks into two groups, a northern group and a southern group, based on geographic location of the beach (**Fig. 4**). Sea Rim (SR) breaks off as sister to the remaining nine northern sites. The Sargent Island sites (SA & SN) break off from the rest of the northern sites at the second node. Padre Island Nation Seashore (PD), which is a geographically southern site (Fig. 1), falls within the northern group in the cluster analysis. The southern cluster includes every southern site with the exception of PD.

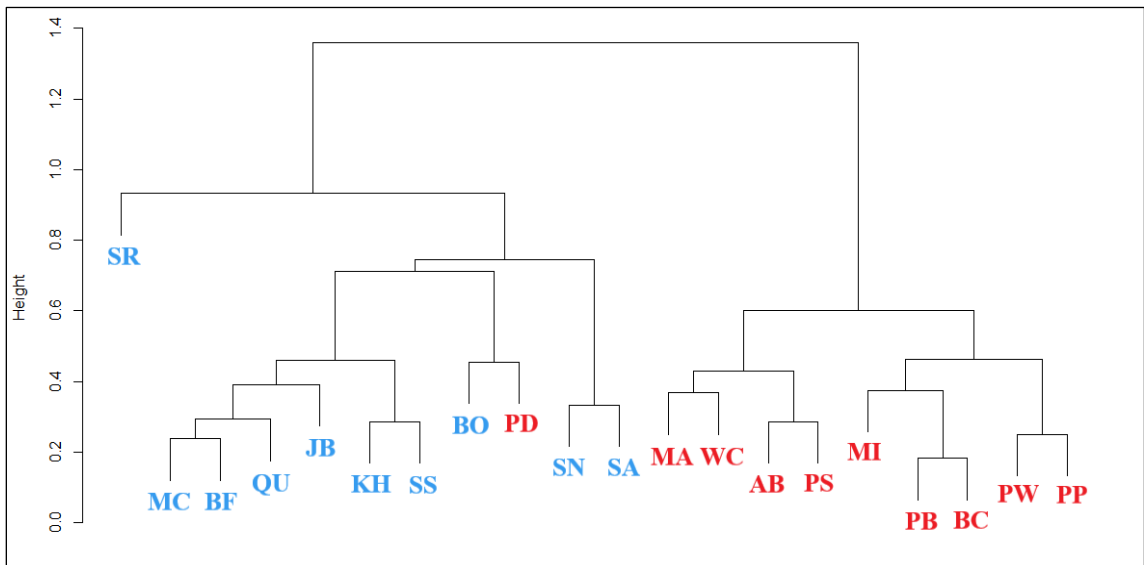


Figure 4 Agglomerative Hierarchical Clustering of Sites

Blue lettering indicates that the site belonged to the northern geographical region. Red lettering indicates that the site belonged to the southern geographical region.

Dune Zone ANOSIM & SIMPER

ANOSIM was used to analyze patterns of similarity between zones based on species abundances. The test yielded a significance value of 0.0001 indicating that there were significant differences found somewhere in the data with dissimilarities ranging from 0.761 to 0.902. The R value found was 0.179. The average dissimilarity between zones was 84.5%. In order to identify between which zones these differences were found a SIMPER test was run. SIMPER analysis displayed the overall percent dissimilarity between pairs of zones (**Table 15**) as well as the primary species that drove any dissimilarity between sites (**Tables 16–18**).

Zone 1 yielded high percentage dissimilarity values of 90.0% and 90.2% when paired with zones 4 and 5, respectively (**Table 15**). Zone 2 also had a high percentage dissimilarity value with zone 5 at an amount of 90.0% dissimilarity.

Table 15 Overall percent dissimilarity between all zone combinations.

	1	2	3	4	5
1					
2	0.778				
3	0.846	0.761			
4	<u>0.900</u>	0.835	0.820		
5	<u>0.902</u>	<u>0.900</u>	0.875	0.832	

SIMPER analysis reveals that the differences between zones 1 and 5 are driven primarily by *S. portulacastrum*, *S. virginicus*, *C. punctatus*, *I. imperati*, *H. subaxillaris*, and *A. psilostachya* (**Tables 17–18**). The differences between zones 2 and 5 are driven

primarily by *C. punctatus*, *S. virginicus*, *H. subaxillaris*, *I. imperati*, *Spartina patens*, and *A. psilostachya* (**Table 18**).

Table 16 The species accounting for the highest contributions to the total dissimilarity between zone 1 and zone 4. Species included are all those species that contributed to dissimilarity up to the point of 70% cumulative contribution.

Species	Average Relative Abundance in Zone 1	Average Relative Abundance in Zone 4	Average Contribution	Standard Deviation of Contribution	Contribution	Cumulative Contribution	p-value
<i>Sesuvium portulacastrum</i>	0.2454	0	12.28%	15.46%	13.66%	13.66%	0.0001
<i>Sporobolus virginicus</i>	0.2044	0.0368	9.84%	8.22%	10.95%	24.61%	0.0072
<i>Croton punctatus</i>	0.1043	0.115	8.49%	10.54%	9.44%	34.05%	0.9597
<i>Ipomoea imperati</i>	0.1683	0.0592	8.45%	9.62%	9.41%	43.46%	0.1985
<i>Heterotheca subaxillaris</i>	0	0.151	7.56%	9.98%	8.41%	51.87%	0.0864
<i>Ambrosia psilostachya</i>	0	0.088	4.42%	6.91%	4.92%	56.79%	0.598
<i>Ipomoea pes-caprae</i>	0.05894	0.0414	4.08%	5.56%	4.54%	61.33%	0.3066
<i>Oenothera drummondii</i>	0	0.0808	4.04%	7.02%	4.50%	65.83%	0.2074
<i>Strophostyles helvola</i>	0	0.0734	3.67%	9.18%	4.08%	69.91%	0.5193
<i>Amaranthus greggii</i>	0.06913	0.00005	3.46%	6.70%	3.85%	73.76%	0.0082

Table 17 The species accounting for the highest contributions to the total dissimilarity between zone 1 and zone 5. Species included are all those species that contributed to dissimilarity up to the point of 70% cumulative contribution.

Species	Average Relative Abundance in Zone 1	Average Relative Abundance in Zone 5	Average Contribution	Standard Deviation of Contribution	Contribution	Cumulative Contribution	p-value
<i>Sesuvium portulacastrum</i>	0.2454	0.00002	12.30%	15.49%	13.65%	13.65%	0.0001
<i>Sporobolus virginicus</i>	0.2044	0.135	11.04%	8.97%	12.24%	25.89%	0.0001
<i>Ipomoea imperati</i>	0.1683	0.0236	8.19%	10.15%	9.09%	34.98%	0.2571
<i>Heterotheca subaxillaris</i>	0	0.143	7.14%	9.11%	7.91%	42.89%	0.1503
<i>Croton punctatus</i>	0.1043	0.0289	5.93%	10.13%	6.57%	49.47%	0.9993
<i>Ambrosia psilostachya</i>	0	0.0953	4.80%	7.34%	5.33%	54.79%	0.4731
<i>Spartina patens</i>	0.03419	0.0697	4.45%	6.50%	4.94%	59.73%	0.3684
<i>Chamaecrista fasciculata</i>	0	0.0760	3.81%	7.68%	4.23%	63.96%	0.33
<i>Panicum repens</i>	0	0.0749	3.75%	10.37%	4.15%	68.11%	0.1897
<i>Amaranthus greggii</i>	0.06913	0.00002	3.47%	6.72%	3.85%	71.96%	0.0078

Table 18 The species accounting for the highest contributions to the total dissimilarity between zone 2 and zone 5. Species included are all those species that contributed to dissimilarity up to the point of 70% cumulative contribution.

Species	Average Relative Abundance in Zone 2	Average Relative Abundance in Zone 5	Average Contribution	Standard Deviation of Contribution	Contribution	Cumulative Contribution	p-value
<i>Croton punctatus</i>	0.304	0.0289	14.80%	13.39%	16.56%	16.56%	0.0384
<i>Sporobolus virginicus</i>	0.0821	0.135	7.91%	8.53%	8.85%	25.41%	0.3103
<i>Heterotheca subaxillaris</i>	0.00630	0.143	7.14%	8.91%	7.99%	33.40%	0.1462
<i>Ipomoea imperati</i>	0.141	0.0236	6.85%	8.20%	7.67%	41.07%	0.6195
<i>Spartina patens</i>	0.0625	0.0697	5.70%	8.89%	6.38%	47.44%	0.0844
<i>Ambrosia psilostachya</i>	0.0241	0.0953	5.26%	7.10%	5.89%	53.33%	0.327
<i>Chamaecrista fasciculata</i>	0.000346	0.0760	3.82%	7.67%	4.27%	57.60%	0.3257
<i>Panicum repens</i>	0	0.0749	3.75%	10.37%	4.19%	61.79%	0.1662
<i>Uniola paniculata</i>	0.0328	0.0444	3.57%	7.71%	3.99%	65.78%	0.2035
<i>Rayjacksonia phyllocephala</i>	0.0613	0.0104	3.36%	6.07%	3.76%	69.54%	0.5357

Dune Zone NMDS

Non-metric multidimensional scaling was performed in order to visualize further differences between zones (**Fig. 5**). The data had a stress value of 0.2376. The joint-plot vectors selected were species richness, species evenness (J), and sandy cover. While zones do not form discrete groupings, they do form a general gradient with zones 1 and 2 falling in the upper right quadrant and zones 4 and 5 in the lower left quadrant. These gradients are influenced by the higher species evenness of zones 1 and 2 and the higher species richness values of zones 4 and 5 (**Fig. 5**).

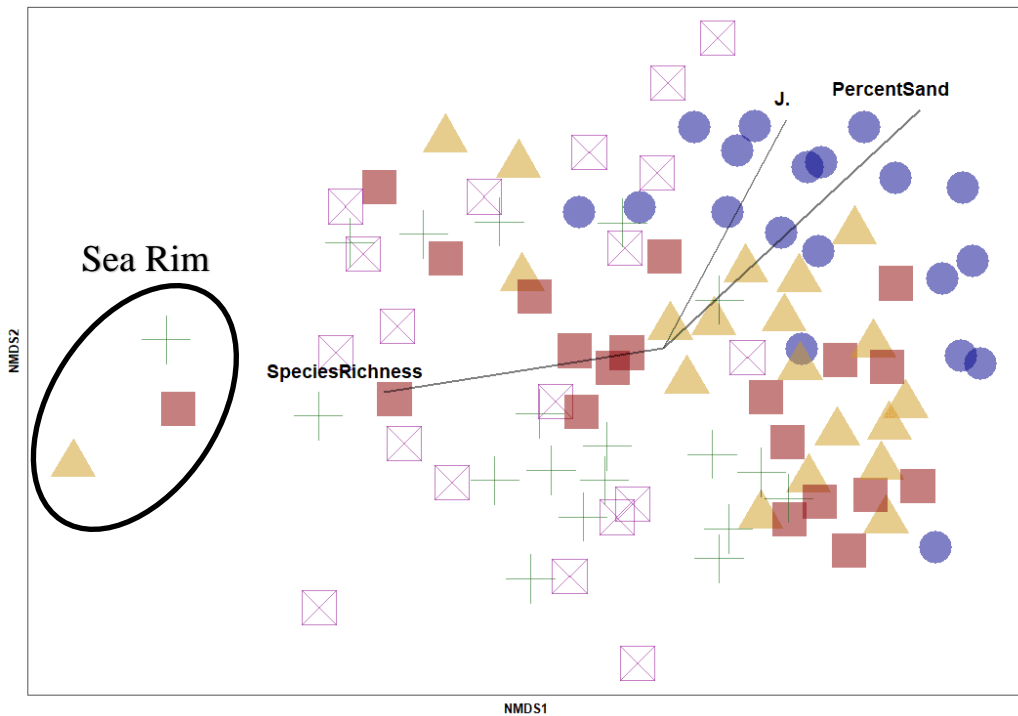


Figure 5 Patterns in Environmental Data across Dune Zones

Blue/Circle = Zone 1 Gold/Triangle = Zone 2 Red/Square = Zone 3
Green/Cross = Zone 4 Purple/X-Square = Zone 5

Site ANOSIM & SIMPER

ANOSIM was used to analyze patterns of similarity between sites based on species abundances. The test yielded a significance value of 0.0001 and an R value of 0.6152, indicating that there were significant differences in species composition between the beaches. Pairwise SIMPER comparisons of dissimilarities ranged from 0.510 to 1 (**Table 19**). The average dissimilarity value between sites was 82.5%. The high average dissimilarity percentage between sites is not uncommon in studies concerning the plant communities of beaches and beach dunes [53, 54]. Based on the high dissimilarity values that can be expected between beach ecosystems [53, 54] a cut-off value of 0.900 was chosen in order to identify unusually dissimilar sites in a dataset that would inherently display high variation. In order to identify between which sites these differences were found a SIMPER test was run. SIMPER analysis displayed the overall percent dissimilarity between a pair of sites (**Table 19**) as well as the primary species that drove any dissimilarity between sites.

Sea Rim State Park (SR) was dissimilar from the largest number of other sites with 15 high dissimilarity values over 90.0% (**Table 19**). Stahlman Park (SS) was dissimilar from the least number of other sites with zero dissimilarity values over 90.0%. Northern Sargent Island (SN) and Southern Sargent Island (SA) were dissimilar from 12 and 11 other sites, respectively. The average number of high dissimilarity values with other sites was 5.15. The average number of high dissimilarity values among northern

sites was 6.09 while the average for southern sites was slightly lower at 4. No southern sites were highly dissimilar from other southern sites.

Table 19 Overall percent dissimilarity (SIMPER) between all site combinations. The cut-off value of 0.900 was used to identify highly dissimilar sites which were made bold and underlined.

	SR	MC	BO	BF	JB	KH	SS	QU	SN	SA	MA	AB	MI	WC	PD	PW	PP	PB	PS	BC
SR																				
MC	<u>0.935</u>																			
BO	<u>0.970</u>	0.851																		
BF	<u>0.921</u>	0.832	0.698																	
JB	<u>0.925</u>	0.691	0.842	0.852																
KH	<u>0.912</u>	0.713	0.828	<u>0.915</u>	0.775															
SS	0.810	0.705	0.862	0.803	0.726	0.701														
QU	<u>0.910</u>	0.833	0.865	0.874	0.768	0.736	0.647													
SN	0.883	<u>0.959</u>	<u>0.945</u>	<u>0.950</u>	<u>0.936</u>	0.835	0.800	0.849												
SA	0.887	<u>0.906</u>	<u>0.927</u>	<u>0.942</u>	<u>0.905</u>	0.803	0.779	0.837	0.692											
MA	0.876	0.841	0.639	0.757	0.879	0.738	0.713	0.858	<u>0.909</u>	0.866										
AB	<u>1.000</u>	<u>0.910</u>	0.648	0.791	0.896	0.876	0.896	0.893	<u>0.976</u>	<u>0.966</u>	0.642									
MI	<u>0.976</u>	0.713	0.815	<u>0.906</u>	0.830	0.784	0.829	<u>0.914</u>	<u>0.920</u>	<u>0.950</u>	0.750	0.816								
WC	<u>0.977</u>	0.739	0.790	<u>0.905</u>	0.815	0.687	0.794	0.890	0.835	0.858	0.729	0.673	0.698							
PD	<u>0.952</u>	0.889	0.739	<u>0.922</u>	0.823	0.852	0.833	<u>0.902</u>	0.717	0.768	0.805	0.833	0.827	0.744						
PW	<u>0.979</u>	0.856	<u>0.914</u>	<u>0.953</u>	0.869	0.827	0.879	<u>0.940</u>	<u>0.966</u>	<u>0.962</u>	0.714	0.898	0.850	0.800	0.889					
PP	<u>0.955</u>	0.848	0.707	0.822	0.875	0.776	0.843	<u>0.929</u>	<u>0.978</u>	<u>0.990</u>	0.564	0.771	0.700	0.743	0.853	0.762				
PB	<u>0.954</u>	0.872	0.749	0.874	0.864	0.849	0.851	<u>0.953</u>	<u>0.948</u>	<u>0.975</u>	0.682	0.817	0.693	0.837	0.778	0.888	0.633			
PS	<u>0.932</u>	0.807	0.653	0.811	0.825	0.731	0.770	<u>0.917</u>	<u>0.966</u>	<u>0.958</u>	0.528	0.708	0.764	0.713	0.770	0.834	0.503	0.564		
BC	<u>0.956</u>	0.768	0.700	0.843	0.785	0.746	0.826	0.840	<u>0.953</u>	<u>0.932</u>	0.680	0.753	0.734	0.785	0.786	0.839	0.675	0.649	0.605	

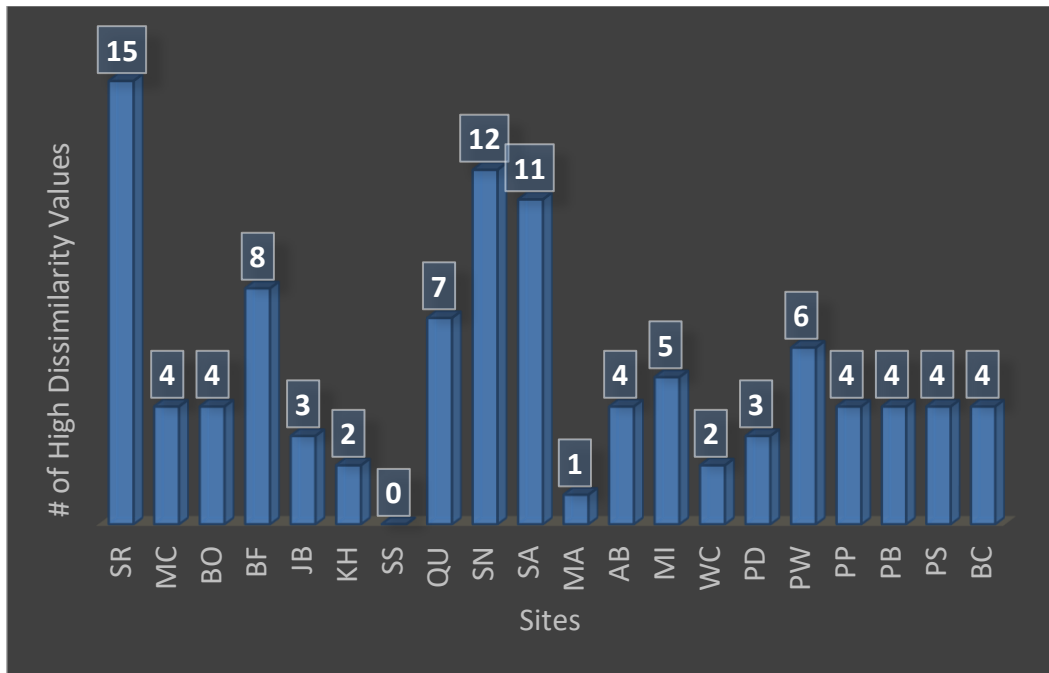


Figure 6 Summary for the High Dissimilarities of Sites

SIMPER produces a list of species and each one's respective contribution toward the total dissimilarity between combinations of zones. This data was summarized in **Table 20** for the combination of Sea Rim (SR) and Aransas Beach (AB) which were identified to have a dissimilarity value of 1, indicating that these two beaches shared no species in common (**Table 19**). *Helianthus argophyllus* Torr. & A. Gray (29.65%) and *Schoenoplectus pungens* (Vahl) Palla (29.32%) were the two species contributing most to the dissimilarity between the sites and were both significant ($p = 0.0001$). *Croton punctatus* also contributed to much of the dissimilarity with 14.22%, but it was not significant.

Table 20 The species accounting for the highest contributions to the total dissimilarity between Sea Rim (SR) and Aransas Beach (AB). Species included are all those species that contributed to dissimilarity up to the point of 90% cumulative contribution.

Species	Average Relative Abundance in SR	Average Relative Abundance in AB	Average Contribution	Standard Deviation of Contribution	Contribution	Cumulative Contribution	p-value
<i>Helianthus argophyllus</i>	0	0.5908	29.65%	2.00%	29.65%	29.65%	0.0001
<i>Schoenoplectus pungens</i>	0.585	0	29.32%	5.92%	29.32%	58.97%	0.0001
<i>Croton punctatus</i>	0	0.2833	14.22%	1.03%	14.22%	73.19%	0.1878
<i>Ambrosia psilostachya</i>	0.151	0	7.63%	7.72%	7.63%	80.82%	0.2495
<i>Sporobolus virginicus</i>	0	0.07308	3.67%	2.01%	3.67%	84.49%	0.6688
<i>Heterotheca subaxillaris</i>	0.0672	0	3.38%	2.84%	3.38%	87.86%	0.8382
<i>Rayjacksonia phyllocephala</i>	0.0605	0	3.02%	4.13%	3.02%	90.89%	0.3249

Regional ANOSIM & SIMPER

ANOSIM and SIMPER were performed with the data being split into northern and southern sites in order to detect any dissimilarities and which species would be contributing to them. Northern and southern regions were separated based on a change in species regime along the coastline (**Table 3**). The test yielded a significance value of 0.0001 with an R value of 0.2873, indicating that there were significant differences found between northern and southern sites. The SIMPER analysis revealed which species were contributing most to the dissimilarity (**Table 21**). *Croton punctatus*, *Heterotheca subaxillaris*, *Ipomoea imperati*, and *Ambrosia psilostachya* accounted for more than one-third of the dissimilarity between northern and southern regions.

An additional regional ANOSIM was performed and included Padre Island National Seashore (PD) in the northern grouping based on the results of the cluster analysis. The ANOSIM produced an R value of 0.258 and a significance value of 0.0001. The R value for this iteration was lower than the initial R value where PD was included in the southern region. This shows that when PD was included in the northern region the dissimilarity between north and south was reduced, suggesting that PD is not similar to other northern sites. For this reason, the geographical approach too defining regions was maintained.

Table 21 The species accounting for the highest contributions to the total dissimilarity between northern and southern sites. Species included are all those species that contributed to dissimilarity up to the point of 70% cumulative contribution.

Species	Average Relative Abundance in North	Average Relative Abundance in South	Average Contribution	Standard Deviation of Contribution	Contribution	Cumulative Contribution	p-value
<i>Croton punctatus</i>	0.1062	0.2045	10.94%	9.01%	12.77%	12.77%	0.0017
<i>Heterotheca subaxillaris</i>	0.0579	0.1257	6.80%	6.63%	7.93%	20.70%	0.0339
<i>Ipomoea imperati</i>	0.0739	0.0913	6.06%	7.75%	7.07%	27.77%	0.9118
<i>Ambrosia psilostachya</i>	0.1075	0.0234	5.75%	7.90%	6.71%	34.48%	0.0093
<i>Sporobolus virginicus</i>	0.0806	0.0724	5.20%	5.53%	6.06%	40.54%	0.7856
<i>Strophostyles helvola</i>	0.0966	0	4.84%	8.25%	5.65%	46.19%	0.0001
<i>Chamaecrista fasciculata</i>	0.0068	0.0789	4.14%	8.25%	4.83%	51.02%	0.0209
<i>Ipomoea pes-caprae</i>	0	0.0774	3.91%	5.46%	4.57%	55.59%	0.0001
<i>Spartina patens</i>	0.0620	0.0204	3.90%	8.36%	4.55%	60.14%	0.2645
<i>Helianthus argophyllus</i>	0	0.0770	3.86%	9.04%	4.50%	64.64%	0.0084
<i>Panicum amarum</i>	0.0718	0.0112	3.81%	5.71%	4.44%	69.08%	0.0040
<i>Oenothera drummondii</i>	0.0360	0.0455	3.57%	6.15%	4.16%	73.24%	0.6719

Site NMDS

Non-metric multidimensional scaling based on species abundances was performed in order to visualize differences between sites (**Fig. 7**). The data had a stress value of 0.1622. The explanatory joint-plot vectors chosen were latitude, longitude, sandy cover, total disturbance value, dune length, and dune height. Latitude and longitude had the strongest effect on the data set, separating the beaches into northern and southern groupings (**Fig. 7**). Total disturbance indicates that certain sites, including both northern and southern examples, are being pulled by a higher than usual disturbance. Dune length and dune height tend towards southern sites while sandy cover tends toward northern sites, however only slightly.

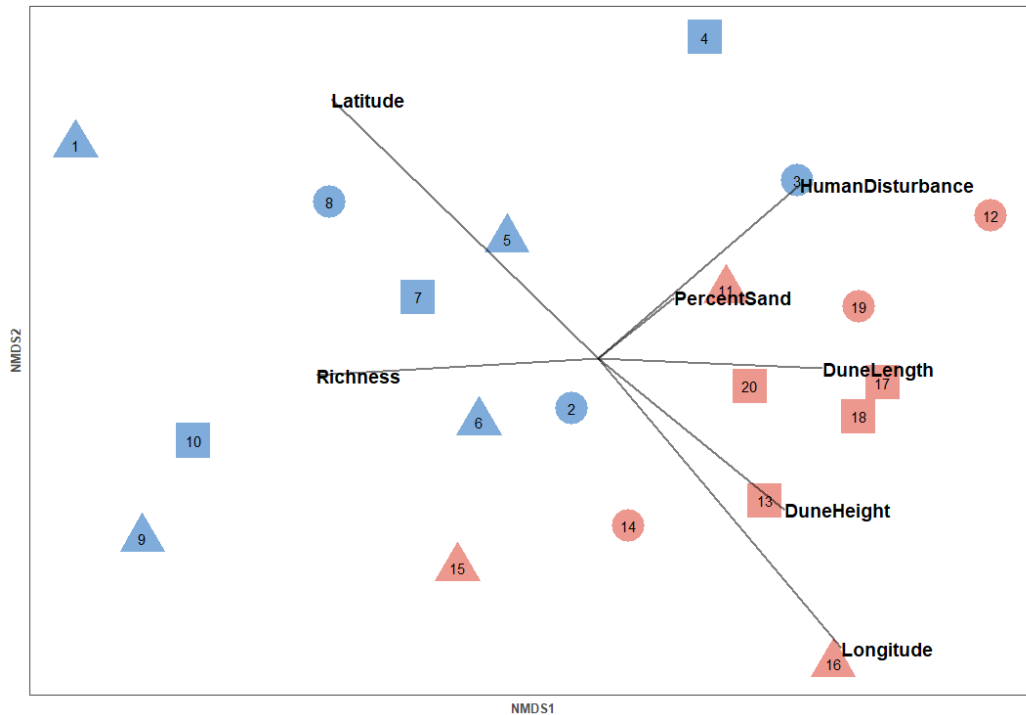


Figure 7 Patterns in environmental data across northern and southern beach sites. Blue shapes represent northern sites and red shapes represent southern sites. Circles represent high disturbance, squares represent medium disturbance, and triangles represent low disturbance. The numbers inside of these circles indicates the site represented by the circle which can be found in **Table 1**.

Dune Zone Indicator Species Analysis

The indicator species analysis for the dune zones determined that there were multiple species indicative of each zone grouping (**Table 22**). The grouping names can simply be interpreted as the zones that they indicator species apply to.

Grouping 1+2 was exemplified by *Sesuvium portulacastrum* and *Amaranthus greggii* S. Watson as indicator species. Grouping 1+2+3+4 was exemplified by *Croton punctatus* and *Ipomoea imperati* as indicator species. Grouping 3+4+5 was exemplified by *Heterotheca subaxillaris*, *Ambrosia psilostachya*, *Oenothera drummondii*,

Strophostyles helvola, and *Chamaecrista fasciculata* as indicator species. Grouping 5 was exemplified by *Solidago sempervirens* L. as an indicator species.

Table 22 Indicator species of dune zone groupings

Grouping of Zones 1+2				
<i>Species</i>	<i>Specificity</i>	<i>Fidelity</i>	<i>IndVal</i>	<i>p-value</i>
<i>Sesuvium portulacastrum</i>	0.9624	0.4000	0.620	0.001
<i>Amaranthus greggii</i>	0.9504	0.3250	0.556	0.003
Grouping of Zones 1+2+3+4				
<i>Species</i>	<i>Specificity</i>	<i>Fidelity</i>	<i>IndVal</i>	<i>p-value</i>
<i>Croton punctatus</i>	0.9652	0.6000	0.761	0.002
<i>Ipomoea imperati</i>	0.9537	0.6000	0.756	0.012
Grouping of Zones 3+4+5				
<i>Species</i>	<i>Specificity</i>	<i>Fidelity</i>	<i>IndVal</i>	<i>p-value</i>
<i>Heterotheca subaxillaris</i>	0.9808	0.5167	0.712	0.001
<i>Ambrosia psilostachya</i>	0.9098	0.4667	0.652	0.002
<i>Oenothera drummondii</i>	0.8717	0.3333	0.539	0.029
<i>Strophostyles helvola</i>	0.9616	0.3000	0.537	0.041
<i>Chamaecrista fasciculata</i>	0.9980	0.2667	0.516	0.010
Grouping of Zone 5				
<i>Species</i>	<i>Specificity</i>	<i>Fidelity</i>	<i>IndVal</i>	<i>p-value</i>
<i>Solidago sempervirens</i>	1.00	0.15	0.387	0.032

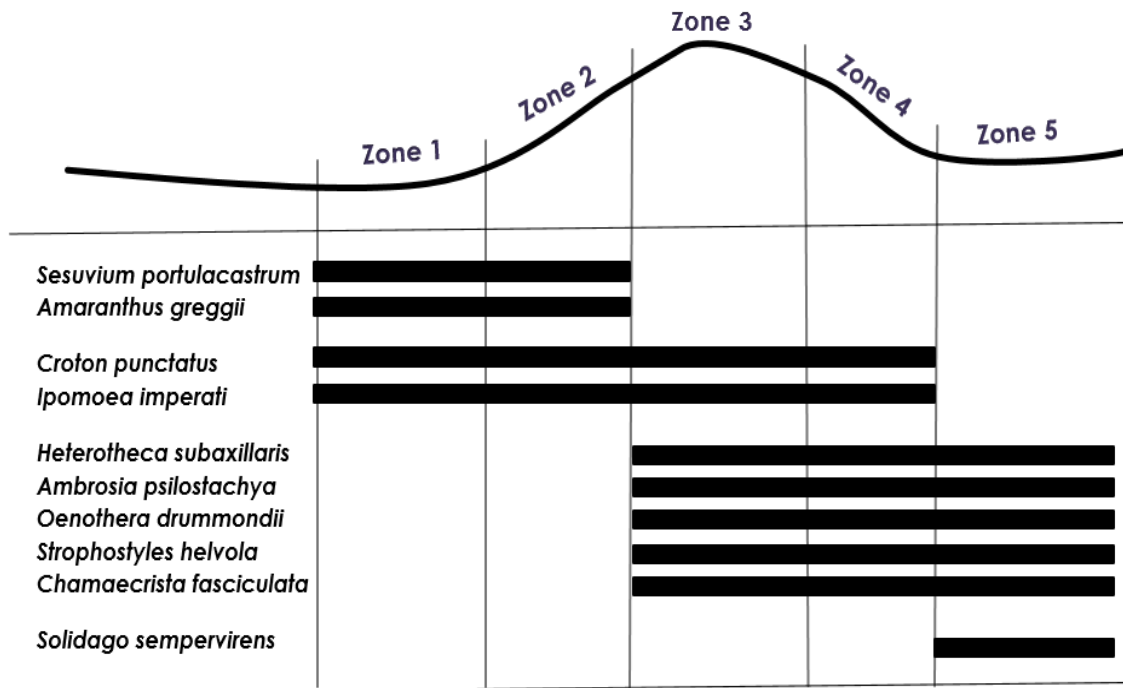


Figure 8 Dune Zone Indicator Species and Corresponding Dune Zone Groupings

Regional Indicator Species Analysis

The indicator species analysis for the northern and southern regions of the Texas Gulf Coast determined that there were multiple species indicative of each region.

The northern complex was exemplified by *Rayjacksonia phyllocephala* (DC.) R.L. Hartm. & M.A. Lane, *Ambrosia psilostachya*, *Panicum amarum*, and *Strophostyles helvola* as indicator species (**Table 23**). *Rayjacksonia phyllocephala* and *S. helvola* both have specificity values of 1.0. *Ambrosia psilostachya* and *P. amarum* yielded high specificity values over 0.850. The fidelity values for all four species were high with the lowest value of 0.7273 belonging to *S. helvola*. IndVals were high for all four species

with values over 0.800. All of the listed species cleared the 0.05 p-value threshold and were statistically significant as indicator species.

Table 23 Indicator species of the northern grouping

<i>Species</i>	<i>Specificity</i>	<i>Fidelity</i>	<i>IndVal</i>	<i>p-value</i>
<i>Rayjacksonia phyllocephala</i>	1.000	0.9000	0.949	0.001
<i>Ambrosia psilostachya</i>	0.8137	0.8000	0.807	0.015
<i>Strophostyles helvola</i>	1.000	0.8000	0.894	0.003
<i>Panicum amarum</i>	0.8834	0.9000	0.892	0.005

Specificity is a component that indicates the probability that the site being observed belongs to the target site group given that the species in question has been located inside of it. **Fidelity** is a component that indicates the probability of the species in question being located in the sites that belong to the target site group. **IndVal** ranges from 0 to 1 with higher values indicating a closer association to the site group.

The southern complex was exemplified by *Ipomoea pes-caprae* as indicator species (**Table 24**). *Ipomoea pes-caprae* possessed a high specificity value of 1.000 and a high IndVal of 0.949. The fidelity value for *I. pes-caprae* was 0.9000. *Ipomoea pes-caprae* cleared the 0.05 p-value threshold and was statistically significant as an indicator species.

Table 24 Indicator species of the southern grouping

<i>Species</i>	<i>Specificity</i>	<i>Fidelity</i>	<i>IndVal</i>	<i>p-value</i>
<i>Ipomoea pes-caprae</i>	1.000	0.9000	0.949	0.001

Human Disturbance Indicator Species Analysis

The indicator species analysis for human disturbance level determined that there were multiple species indicative of certain disturbance groupings (**Table 25**). Medium disturbance was exemplified by *Chamaecrista fasciculata* as an indicator species. High disturbance was exemplified by *Helianthus argophyllus* as an indicator species. The grouping of low and medium disturbance was exemplified by *Ambrosia psilostachya* as an indicator species.

Every indicator species for human disturbance had high specificity values of over 0.900 and low fidelity levels of lower than 0.500. IndVals ranged from 0.515 in *H. argophyllus* to 0.638 in *A. psilostachya*. All of the listed species cleared the 0.05 p-value threshold and were statistically significant as indicator species.

Table 25 Indicator species for varying levels of human disturbance

Medium Disturbance

<i>Species</i>	<i>Specificity</i>	<i>Fidelity</i>	<i>IndVal</i>	<i>p-value</i>
<i>Chamaecrista fasciculata</i>	0.9103	0.3810	0.589	0.0057

High Disturbance

<i>Species</i>	<i>Specificity</i>	<i>Fidelity</i>	<i>IndVal</i>	<i>p-value</i>
<i>Helianthus argophyllus</i>	0.9553	0.2778	0.515	0.0105

Grouping of Low and Medium Disturbance Levels

<i>Species</i>	<i>Specificity</i>	<i>Fidelity</i>	<i>IndVal</i>	<i>p-value</i>
<i>Ambrosia psilostachya</i>	0.9001	0.4524	0.638	0.0396

CHAPTER 5-DISCUSSION

General Research Objectives

The main objectives of this study were to identify and characterize community types by dune zone, to identify indicator species for regions of the Texas coastline, and to examine the effect of disturbance on Texas beach species composition.

Dune Zones as Community Types

Vegetation patterns of Texas beaches follow a distinct pattern along transects from the vegetation line to the backdune. ANOVA testing found that percent sandy cover decreases from zone 1 to zone 5 (**Tables 6, 12, & 13**). Zones increase in percent vegetative cover (**Tables 14 & 15**) and richness (**Tables 10 & 11**) from zone 1 to zone 5 (**Table 6**). Average Pielou's Evenness values did not form a noticeable trend (**Table 6**). Dune zones appear to be placed within distinct boundaries but actually tend to form a gradient of conditions and species composition. The NMDS for dune zones reflects a gradient of community composition and environmental conditions (**Fig. 5**). The vectors of evenness (J) and percentage of sand indicate higher levels toward the upper right-hand corner. Higher levels of species richness are associated with the leftward side of the plot. Dune zones 1 and 2 had most of their points clumped together in the upper right quadrant (**Fig. 5**). Zones 3, 4, and 5 were scattered throughout the lower left quadrant (**Fig. 5**). The placement of points on the NMDS plot reflect the findings of the ANOVA testing

that found significant differences in percent sand and species richness between zones (Tables 10–13).

Dune Zone 1 (The Vegetation Line)

The most distinct dune community type is dune zone 1, the vegetation line. This zone is defined by the highest percentage of sand, the lowest percentage of vegetation, and the lowest species richness (Tables 6, 11, 13, & 15). Lower species richness can be expected in zone 1 (Table 11), most likely due to the higher rates of stress and disturbance associated with closer proximity to the shoreline [2, 6, 19]. The species composition of zone 1 is statistically different from zones 4, and 5 based on ANOSIM analysis (Table 15). SIMPER analysis identified *Sesuvium portulacastrum*, *Sporobolus virginicus*, and *Ipomoea imperati* (Tables 17–19) as the three species that contributed the most to the separation of between zones 1 with zones 4 and 5 in the NMDS (Fig. 5). Indicator Species Analysis identified *S. portulacastrum* and *A. greggii* as indicator species for the grouping of dune zones 1 and 2 (Table 22). *Croton punctatus* and *I. imperati* were indicators of the grouping of zones 1, 2, 3, and 4.

Sesuvium portulacastrum, an important pioneer and dune building species [7, 14 60], occurs in zones near the vegetation line (zones 1 and 2) and declines in abundance towards the backdune (Table 4) with seeds that can remain viable after prolonged exposure to salt water [3]. This pattern of distribution has been noted from studies of the Gulf Coast beaches of Mexico [6, 7, 51]. *Sporobolus virginicus* is known as a pioneer and dune building grass and is commonly found near species such as *S. portulacastrum*

and *A. greggii* [6, 7, 51, 60] and exhibits enhanced growth potential in the presence of salts as well as specialized glands meant for removal of excess salts [11, 21, 59].

Ipomoea imperati is commonly associated with *S. portulacastrum*, *A. greggii*, and *S. virginicus* as a pioneer species located at or near the vegetation line but can also be found further inland [51] and has seeds that remain viable after prolonged exposure to salt water [3]. *Croton punctatus* is notable as a soil binder and pioneer species in dunes and helps to stabilize the dune in zone 2 and subsequent zones [6, 60]. Both *I. imperati* and *C. punctatus* occur in the beaches of Mexico [7, 14, 51]. *Amaranthus greggii* is an indicator species for zones 1 and 2 (**Table 22**). *Amaranthus greggii* is an important annual colonizer [13, 60]. The presence of *A. greggii* in zones 1 and 2 and its decline towards the backdune has been noted in the Gulf Coast beaches of Mexico [6, 51]. Each of the species mentioned have halophytic adaptive traits for salt-resistance. *Amaranthus greggii* has not yet been shown to have beneficial adaptations against salinity but instead exhibits adaptations for combating sand accretion and seedlings that can germinate at low depths [3, 51]. The adaptations that these species exhibit reflect the stress and disturbances of the zone which they inhabit that is often defined by extreme halophytes and accretion-resistant pioneer species [6, 19, 51].

Dune Zone 2 (The Windward Slope)

Zone 2 defines the distinctive community type of the windward slope of a dune. From zone 1 to zone 2 stresses and disturbances are reduced and species richness and percentage of vegetation increase (**Tables 6, 10, & 11**). Zone 2 experiences a change in

species composition because even small changes in distance will open an area up to new species that could not handle the conditions of nearby zones [55]. ANOSIM found zone 2 to be highly dissimilar to zone 5 (**Table 15**) and SIMPER indicated the species mostly contributing to the dissimilarity are *C. punctatus*, *S. virginicus* from zone 2 and *H. subaxillaris* from zone 5 (**Table 18**). Indicator species for this zone are the same as those for zone 1 (**Table 22**).

Dune Zones 3 and 4 (The Crest and the Leeward Slope)

Dune zones 3 and 4 define a community type characterized by similar levels of sand, vegetative cover, and species richness (**Table 6**). In ANOVA testing of differences in percent of vegetative cover, zones 3 and 4 were the only zones not to be significantly different in that aspect (**Table 14**). They are both set apart from dune zone 2 by a continued shift in stress and disturbance that makes the conditions of zones 3 and 4 unlike the windward slope [3, 47]. They are also set apart from dune zone 5 because of the same continual shift in conditions [2, 55]. Indicator species analysis did not reveal a distinctive indicator species for this community type but the groupings it created can be used to infer that dune zones 3 and 4 are best defined as transitional between zone 2 and zone 5. ISA revealed a grouping of dune zones 1, 2, 3, and 4 (**Table 22**). This grouping begins at the vegetation line and extends through every zone that is found on the dune itself while excluding zone 5. The indicator species of this grouping, *C. punctatus* and *I. imperati*, are common in the first two community types as well as in the current one. ISA revealed another grouping of dune zones 3, 4, and 5 (**Table 22**). This grouping begins at

the crest and extends through the backdune while excluding the introductory zones. The indicator species of this grouping, *H. subaxillaris*, *A. psilostachya*, *O. drummondii*, *S. helvola*, and *C. fasciculata*, are shared by this community type as well as the final community type. Dune zones 3 and 4 act as a compositional “bridge” between the highly disturbed and stressed zone 2 and the very stabilized and less stressed zone 5. This is exhibited in the appearance of zones 3 and 4 in multiple ISA groupings with their adjacent zones.

Dune zones 3 and 4 are found in more sheltered areas of the beach (zone 3 on the dune crest and zone 4 on the leeward slope) and represent an intermediate area between zones 1 and 2 and zone 5 in terms of percent sandiness, percent vegetative cover, and species richness. Indicator species analysis found that zones 3 and 4 share *H. subaxillaris*, *A. psilostachya*, *O. drummondii*, *S. helvola*, and *C. fasciculata* with zone 5 (**Fig. 8**). *Heterotheca subaxillaris* and *S. helvola* experience high rates of decay and death with prolonged exposure to salinity and are better fit for these zones which are most sheltered from the effects of salt spray [64]. *Ambrosia psilostachya* has been found to be more abundant in areas with intermediate levels of disturbance [65]. This supports *A. psilostachya*'s increased abundance in zone 3 and onward as the level of disturbance decreases from that of zones 1 and 2 [2, 6, 19]. *Oenothera drummondii* is recorded as being more abundant in sheltered areas where salt spray is reduced, and the dune has already been established with the help of pioneer species [7].

Dune Zone 5 (The Backdune)

Dune zone 5 defines the backdune community type. Zone 5 had the highest species richness, the highest percentage of vegetative cover, and the lowest amount of sand (**Table 6**). ISA identified *Solidago sempervirens* as the sole indicator species for zone 5. *Solidago sempervirens* was 100% specific (Specificity =1.00) to zone 5 (**Table 22**). Eight other species had a 100% specificity value with zone 5, however, they typically only occurred a single time and were not significant indicators. *Solidago sempervirens* is a halophyte and does possess some amount of salt tolerance but responds very negatively to small increases in salt concentration [50]. Compared to other halophytes known to possess greater salt tolerance, such as *Ipomoea imperati* and *Sesuvium portulacastrum* which grow naturally at the forefront of the dune or vegetation line, *Solidago sempervirens* is more reserved in its ability to combat salt and has adapted for a position further behind the dune so it can continue to benefit from its preferred sandy soils while also avoiding the higher salt concentrations that curtail its biomass [50].

Regional Trends

The Direct Gradient table indicated that the Texas coastline can be divided into two regions: a northern regime of species that remain common from sites 1–10 and a southern regime of species that remain common from sites 11–20 (**Table 3**). The point of separation between north and south was somewhat arbitrary because the change in species regime was gradual. Matagorda Beach (MA) appeared to be the first site to include uniquely southern species. A cluster analysis was performed to identify whether

or not this separation was justified (**Fig. 4**). The resulting cluster tree revealed that the chosen separation between northern and southern sites was justified as sites belonging to each region were clearly grouped differently. The sole exception to this was the placement of Padre Island National Seashore (PD) within the northern grouping.

The NMDS plot for sites reflected this geographic trend and the two largest explanatory vectors were latitude and longitude (**Fig. 7**). Southern beaches tended to group in the lower right-hand quadrant, whereas Northern beaches were considerably more scattered throughout the plot. The tightest cluster of sites is between sites 17 (PP), 18 (PB), 19 (PS), and 20 (BC) which indicates a fair amount of consistency in the community composition in beaches belonging to the southernmost Texas coastline. Site 1 (SR) located in the top-left was quite distant from any other site, both horizontally and vertically, suggesting that it has a community composition unique from the other sites. Sites 9 (SN) and 10 (SA) were both located on Sargent Island and cluster together in the bottom left corner. Site 12 (AB) is the furthest right on the x-axis.

Indicator species analysis identified *Rayjacksonia phyllocephala*, *Ambrosia psilostachya*, *Strophostyles helvola*, and *Panicum amarum* as indicator species for the northern sites (**Table 23**). *Rayjacksonia phyllocephala*, *A. psilostachya*, and *S. helvola* are prevalent in the northern sites and virtually absent in the southern sites with the sole exception being a small resurgence of *A. psilostachya* in one southern site. The ranges of *R. phyllocephala* and *S. helvola* appear to end on Sargent Island (SN & SA) (**Table 3**). The range of *A. psilostachya* appears to end on Matagorda Island, although it does appear

in Padre Island Seashore (PD) as well, indicating that its range extends further south but at lower frequencies or that it is may be spread by human involvement. The distribution of *P. amarum* is particularly interesting. While ISA indicated that it is a Northern indicator species, it is found in Southern Texas and its range extends down to the state of Campeche [2, 6, 7, 14]. It appears that *P. amarum* exhibits a much higher abundance in northern Texas before steadily decreasing from the southern region of Texas along the Gulf Coast of Mexico to the state of Campeche.

The ISA identified *I. pes-caprae* as the sole southern indicator species (**Table 23**). *Ipomoea pes-caprae* was seen exclusively in southern sites. *Ipomoea pes-caprae* is found in every Mexican Gulf Coastal state from Tamaulipas to Quintana Roo [2, 6, 7, 14]. Correspondingly, the Northern indicator species of *R. phyllocephala*, *A. psilostachya*, and *S. helvola* do not occur in Mexico.

Sea Rim

Sea Rim displayed a markedly higher amount of dissimilarity from other sites. Sea Rim (SR) and Aransas Beach (AB) had the highest dissimilarity percentage between any site combinations. SR also had the largest amount of high dissimilarity rankings with other sites with 15 and averaged 93.2% dissimilarity across all site comparisons (**Table 19**). Cluster analysis showed that, while Sea Rim is adjoined to the northern grouping of sites, it does maintain a degree of distinction from the rest of the northern sites (**Fig. 4**). This is a unique beach habitat in that it deviates from the expected norms of coastal beach habitats in many ways. Usually a determinable dune is not present and when one is it is

still extremely low (**Table 5**). Across the majority of the beach there is not a noticeable change in elevation from the swash zone to the backdune with the result that the marsh species expand into the beach habitat. The difference in composition can be seen in **Fig. 5** where three of Sea Rim's data points stand apart from the remaining data points.

Sea Rim possesses a unique suite of plants that were either unique to it, or that were very rarely found at other beaches, including: *S. pungens*, *P. vaginatum*, *C. esculentus*, *V. luteola*, *E. prostrata*, and *A. indica* (**Table 3**). All of these species are known for their association with marsh habitats [66, 67, 68, 69, 70]. The primary species that indicated the uniqueness of Sea Rim was *Schoenoplectus pungens* which is a species usually associated with marshes and areas with brackish water [55]. This is due to the beach's close proximity to an extensive range of marshlands that begin only a few meters further inland.

In the last 15 years, Sea Rim has been hit by Hurricanes Katrina, Rita, Ike, and Harvey. The combined effect of these major disturbances may have contributed to the drastically reduced dunes that the site currently exhibits and prevented new dunes from forming. The effects of these hurricanes could also have led to the expulsion of plant species that used to be present in the area and their replacement with the marsh vegetation that now dominates the site.

Sargent Island

The two Sargent Island sites (SN & SA) exhibit the second and third largest amount of high dissimilarity values with Northern Sargent (SN) being highly dissimilar

from 12 other sites and Southern Sargent (SA) being highly dissimilar from 11 (**Table 19**). Cluster analysis separated the Sargent Island sites into their own solitary node (**Fig. 4**). These two sites were the final sites to be designated as part of the northern composition of species before a new species composition takes hold in the southern sites. The Sargent Island sites exhibit 3 species that do not appear in in any other site (*Cyperus odoratus* L., *Aphanostephus skirrhobasis* (DC.) Trel., and *Tidestromia lanuginosa* (Nutt.) Standl.), 3 species that were common in the north and subsequently stop appearing after Sargent Island (*R. phyllocephala*, *S. helvola*, and *S. sempervirens*), and 2 species that did not appear before Sargent Island but recurred in the southern sites (*Physalis cinerascens* (Dunal) Hitchc. and *Chamaesyce maculata* (L.) Small) (**Table 3**). These uniquely Sargent Island species as well as the species that either began or ended their range on Sargent Island suggest that Sargent Island may be a potential ecotone between the northern and southern floral regimes of Texas' Gulf Coast.

Aransas Beach

Aransas Beach (AB) was notable for high disturbance (**Table 2**) and the lowest species richness across all sites (**Table 7**). While other sites shared a high rate of human disturbance, Aransas differed in the intensity of these disturbances. Aransas was the single site to have what can only be described as dedicated “lanes” for traffic, wooden posts erected for parking and separation of the swash zone from the “traffic lanes”, and heavy machinery fortifying dunes in certain stretches of the beach. Dunes were also extremely high, 6.00 meters on average. Aransas Beach was also struck by some of

Hurricane Harvey's strongest winds in 2017, experiencing gusts as high as 59 m/s [61]. In certain cases, the reductions in species richness that are caused by hurricanes can take two or three years to return to normal [58]. Hurricane Harvey had made landfall with Aransas Beach just over two years prior to the time of data collection. This places Aransas Beach well-within a timeframe of continued recovery from a storm of Hurricane Harvey's magnitude, potentially explaining the reduced species richness [58]. Ultimately, the abnormalities of the site may be due to either the human disturbance, the hurricane's effect, or a compounded result of both.

Bolivar Peninsula & Padre Island National Seashore

Cluster analysis grouped the geographically southern Padre Island National Seashore (PD) within the northern grouping and placed it as sister to Bolivar Peninsula (BO) (**Fig. 4**). Additional evidence for this result comes from NMDS, in which Padre Island National Seashore (site 15) pulls away from other southern beaches and towards the northern beaches (**Fig. 7**). The apparent similarity between PD and BO can be explained through discrepancies between their species compositions and regional indicator species. BO and PD were both missing the northern indicator species of *Rayjacksonia phyllocephala* and *Strophostyles helvola*. Both BO and PD possessed the northern indicator species, *Ambrosia psilostachya*. Neither site possessed the southern indicator *Ipomoea pes-caprae*.

In order to further analyze this grouping an additional ANOSIM was performed which found that by adding PD into the northern grouping the dissimilarity between north

and south was reduced from R value of 0.2873 To 0.258. These results suggest that placing PD in the southern group is justified.

Human Disturbance

ANOSIM was performed for human disturbance categories and yielded the very small R value of 0.05. This low R value is extremely close to 0, indicating that dissimilarities between disturbance categories are not different from the dissimilarities within disturbance categories. For this reason, the ANOSIM and SIMPER analyses for human disturbance categories were considered uninformative and excluded. The NMDS for sites (**Fig. 7**) did not reveal a geographic cause for human disturbance as sites of varying levels of disturbance were scattered throughout the plot. Indicator species analysis did reveal species that are important in different human disturbance categories. The lack of useful results from ANOSIM, SIMPER, and NMDS contrary to the pertinent findings of the ISA suggest that while human disturbance categories do not affect patterns in overall species composition they do affect abundance and frequency of certain indicator species.

Ambrosia psilostachya was identified as the indicator species of low and medium disturbance levels. A specificity value of 0.9001 (**Table 25**) indicates that when *A. psilostachya* was found there would be a 90% chance that it would be in an area of low or medium disturbance. This supports previous findings that *A. psilostachya* is most abundant in areas of intermediate disturbance [65]. Additionally, *A. psilostachya* was also an indicator species of the grouping of zones 3, 4, and 5 (**Table 22**). These zones

exhibit a medium level of disturbance with regards to the spatial position on the dune system [2, 6, 19]. The inclusion of the low level of human disturbance in this grouping could imply that *A. psilostachya* is not as reliant on medium levels of disturbance as has been suggested [65] and can thrive without the impacts of disturbance. The inclusion of low disturbance could also be indicative of the natural and perpetual disturbance that affects all beach dunes. In which case, *A. psilostachya*'s affinity for medium levels of disturbance would be inherently suited to the beach environment. *Ambrosia psilostachya*'s range was mostly limited to the northern Texas Gulf Coast which it was also an indicator species of (**Table 23**). Therefore, *A. psilostachya*'s relevance as an indicator of medium disturbance is restricted to the northern coast of Texas.

Chamaecrista fasciculata was revealed as the indicator species of medium levels of human disturbance. As opposed to *A. psilostachya*, *C. fasciculata* was an indicator of solely medium disturbance levels. *Chamaecrista fasciculata* has been noted as being prone to disturbed areas, but the levels of disturbance have not been measured [71, 72]. This helps to categorize it similarly to *A. psilostachya* as a species that may prefer medium disturbance while avoiding high disturbance. *Chamaecrista fasciculata* appeared sporadically along the Texas coastline in a total of 8 sites (3 northern sites & 5 southern sites) (**Table 3**). Having a range that includes both northern and southern sites makes *Chamaecrista fasciculata* a more usable indicator species of medium disturbance along the entire Texas coastline.

Helianthus argophyllus was found as an indicator species of high levels of human disturbance. *Helianthus argophyllus* carried a specificity above 0.9553 indicating that when it was seen there would be a 95.53% chance that it was within a location with high human disturbance (**Table 25**). *Helianthus argophyllus* is able to combat the stresses of the beach environment as other beach species do, but this would suggest that it is more able to survive intense disturbance regimes than other plants. *Helianthus argophyllus*'s low fidelity value of 0.2778 indicates that it is not necessarily a commonly found species as it was only seen in 27.78% of sites with high human disturbance. Taking both of these values into account, *H. argophyllus* can be summarized as a species that is highly indicative of high human disturbance, but still uncommon throughout the Texas Coastline. It is also notable that *H. argophyllus* was only located in southern sites and may be revealed as a more common indicator of high human disturbance with specificity to the southern region of Texas. Current literature on *H. argophyllus* does not focus on the disturbance tolerance of the species. Occasionally, the drought tolerance of the species is mentioned when referring to benefits of hybridization between sunflowers [62]. Furthermore, literature discussing *H. argophyllus*'s potential uses in recolonization of dunes after hurricanes is nonexistent.

Significance

The findings of this study conclude one of the largest studies of Texas Gulf Coast's floral composition that spans the entire Texas coastline. This study provides a record of the species that inhabit much of Texas' Gulf Coast as well as their abundances

and ranges. Data found can be used as a point of comparison for future studies that seek to observe changes in species composition, abundances, and ranges after serious disturbance events such as hurricanes or human development. The analysis of differences in the species compositions of sites identified multiple abnormal beaches of the Texas Gulf Coast including Sea Rim, which provides a look into the unique interaction of marshlands and coastline, and Aransas Bay, which provides important observations of the effects of intense human disturbance. A gradient of species from the northern coast to the southern coast was identified as well as a potential region of transition between the regimes in Sargent Island. This study provides an in-depth analysis of the foredune complex and details where on the foredune certain species are specially adapted for. Many studies neglect to mention where in relation to the foredune each species is found [35], and instead generalize the habitat of the plant as “coastal” [2], “beach” [3, 53], or a broad designation of some sort of dune type [3, 19, 35, 52, 55, 57]. This is particularly true for studies focusing on Texas beach dunes where the preferred dune zone of species is rarely recorded [45, 46, 47, 60].

CHAPTER 6-LITERATURE CITED

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