

**PLANT ASSEMBLAGE STRUCTURE ON BARRIER ISLAND  
'PIMPLE' DUNES AT THE VIRGINIA COAST RESERVE  
LONG-TERM ECOLOGICAL RESEARCH SITE**

by

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## **ABSTRACT**

### **PLANT ASSEMBLAGE STRUCTURE ON BARRIER ISLAND 'PIMPLE' DUNES AT THE VIRGINIA COAST RESERVE LONG-TERM ECOLOGICAL RESEARCH SITE**

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The habitats at the VCR LTER that were the focus of the current study are the Hog Island and Parramore Island 'pimples', small, rounded dunes forming along main dune ridges of the barrier islands. There are distinct plant assemblage zones found on pimples, although most of these dunes are 10 – 20 m in diameter. Hypotheses of the study were that fresh water availability was a main determinant of differences between assemblages and that pimple size and location would influence diversity and assemblage structure. Research goals were 1) to describe the plant assemblages on pimples, 2) to relate edaphic and geomorphological factors to pimple assemblage diversity and composition at different spatial scales, and 3) to compare assemblage – environment interactions on pimples and main dune ridges. Accomplishing these goals entailed field vegetation surveys of a representative sample of pimple and dune plant assemblages and environmental monitoring. There were distinct assemblage types that segregated themselves by habitat type: marsh, shrub thicket, and dry summit. Shrub assemblages were less diverse than either marsh or summit habitats. There was no relationship between pimple size and diversity or location. Differences in diversity and composition

among pimples were as great as differences among transects within pimples. Pimple diversity and species composition were different from the main dunes. Fresh water availability was important in differentiating differences, both among transects and among species, but it was not the only important factor. Nutrients, such as boron, were also important in describing variation among species. It is likely that interactions between water and other factors (e.g. the accumulation of some mineral nutrients in the marsh after they are leached from the dune summits) are the most important determinants to species abundances. A secondary goal was to evaluate ordination techniques used in pattern detection throughout the study. Canonical correspondence analysis and non-metric multidimensional scaling performed best overall. CCA, which is a direct gradient analysis, described groups of transects and species that largely matched my *a priori* assumptions. Furthermore, it provided correlation data about species – environment relationships that were equivalent to multiple regression. NMS, a distance-based, indirect-gradient method, described high percentages of variation (> 80 %) in the first two or three axes, but relationships between environment and species abundances had to be inferred. Bray-Curtis ordination and especially principal components analysis did not explain as much variation in the data.

This thesis is dedicated to M.E.M., T.A.M., and R.D.B.

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## CHAPTER 1

### INTRODUCTION

#### BARRIER ISLAND ECOLOGY

The factors influencing plant assemblages on dunes and barrier islands were among the first subjects of interest to ecologists, one of the most notable being Cowles (1899), who first described the process of floristic succession based on observations of forest structure on the dunes of Lake Michigan. Because they are created by winds, tides, and currents, barrier islands are geomorphologically and biologically dynamic. Storms, for example, can create new dune ridges or wipe out old ones overnight (Dolan and Hayden 1981, Dolan et al. 1988, Kochel and Wampfler 1989). The interaction and fluctuation of geomorphology, storms, hydrology, topography, and nutrient availability on barrier islands make plant assemblages change rapidly relative to most mainland systems.

#### *Geomorphology and storms*

Topography on barrier islands typically includes a conspicuously parallel sequence of dune ridges. These form as storms, tides, and wind deposit sand and create new foredunes, which are subsequently stabilized by colonizing plants (Cowles 1899, Godfrey et al. 1979, Roman and Nordstrom 1988, Ehrenfeld 1990, Hayden et al. 1995, Anthonsen et al. 1996, Bate and Ferguson 1996, Rust and Illenberger 1996, Fearnough et al. 1998, Lichter 1998). The age of these dune ridges can be estimated through radiodating; cartographic, historical, and meteorological records; and remotely-sensed data, such as aerial survey photographs. Researchers use this evidence to establish a

‘chronosequence’ of dune ages across islands (Ehrenfeld 1990, Hayden et al. 1991, Hayden et al. 1995, Day et al. 2001).

The effects of both salinity and flooding make storms a major force in shaping barrier island plant communities. Salt spray can travel across entire islands during severe storms, impacting interior species with low salinity tolerance (Ehrenfeld 1990). Saline flooding from storm surges has an even greater impact on salt-intolerant species (Ehrenfeld 1990, Young et al. 1994, Young et al. 1995a, Young et al. 1995b, Hester et al. 1996, Houle 1997). Storm surges and wind can either bury or wash away entire plant assemblages as sand is deposited or eroded; dune plant species respond with adaptations including increased growth rates, enhanced CO<sub>2</sub> uptake, enhanced germination, and varied biomass allocations between above and belowground tissue, depending on survival strategy (Weller 1989, Yuan et al. 1993, Erickson 1994, Young et al. 1994, Erickson and Young 1995, Brown 1997, Perumal and Maun 1999). The relative importance of salinity tolerance and burial tolerance to the structure of plant assemblages has been studied, but results are equivocal and often species-specific (Schroeder et al. 1979, Young et al. 1995a, Young et al. 1995b, Bate and Ferguson 1996, Rust and Illenberger 1996, Dilustro and Day 1997, Ehrenfeld 1997).

#### *Importance of land and water surfaces*

On barrier islands, seemingly minute elevation changes can have a dramatic effect on water availability and water quality, both of which directly influence biological communities (Hayden et al. 1995, Zou et al. 1995, Lammerts et al. 2001, Muñoz-Reinoso 2001). Several processes, including evapotranspiration, astronomical and wind-driven tides, rainfall and drought, influence the amount of surface and ground water available on

barrier islands and the salinity of that water. This is a major, if not the most important, determinant of vegetation assemblage structure (Ehrenfeld 1990, Young et al. 1994, Hayden et al. 1995, Tolliver et al. 1997).

Underground freshwater percolating into the soil from rain forms a lens-shaped zone of saturation that floats on denser saline water derived from overwash or lateral infiltration from the ocean. Theoretically, such a lens can form on a sand island of any size, whether a pimple mound or a coastal barrier. It develops because of a combination of rainwater infiltrating across the island and groundwater seepage discharging into bodies of water around the island edge. Thus, a sand dune by itself may not affect the elevation of the water table beneath it, but rather a dune (or pimple mound) flanked by permanent water bodies is likely to generate a relatively high elevation on the water table surface (Whittecar and Emry 1992).

The depressions between successive dune ridges, 'slacks' or 'swales', are prone to flooding and often contain marsh communities. A distinct boundary between plant species assemblages often exists at the junction of dunes and swales (Jones and Etherington 1971, Godfrey et al. 1979). This is the result of differing abilities to withstand the effects of flooding, primarily anoxia and mineral poisoning (e.g., from  $\text{Fe}^{++}$ ,  $\text{Mn}^{++}$ , or sulfides) related to chemically reduced conditions (Jones and Etherington 1971, Jones 1972a, 1972b, 1975a, 1975b, Studer-Ehrensberger et al. 1993). Salinity of water in a swale marsh varies with elevation and exposure to tides and storm overwash. Assemblages within and bordering the marsh are structured as a consequence of resident species' relative tolerances to salinity and desiccation (Godfrey et al. 1979, Young et al. 1994, Hayden et al. 1995, Young et al. 1995a).

### *Nutrient availability*

In addition to periodic disturbance and changing microtopography, nutrient availability influences community structure and function on barrier islands (Ehrenfeld 1990, Young et al. 1992, Verhoeven et al. 1996). In island ecosystems, patchy availability of nutrients, especially nitrogen and phosphorus, influences species composition and above and belowground biomass. Nutrient cycling is consequently tight, with most nutrients sequestered in biomass (Day 1996, Stevenson and Day 1996, Verhoeven et al. 1996, Dilustro and Day 1997).

The well-drained, sandy soils on coastal dunes have high leaching rates of nitrate from the upper layers of the soil (Kachi and Hirose 1983, Sande and Young. 1992, Verhoeven et al. 1996, Wijnholds and Young 2000). Cation-exchange capacity and, hence, availability of most mineral nutrients are limited due to the low organic matter and clay content of the soil (Brady and Weil 2002). Stressful conditions in dune soils, such as low fresh water availability, may also inhibit nitrification and nitrogen mineralization (Kachi and Hirose 1983).

In contrast to dunes, nutrient availability in swales is limited by an overabundance of water. Flooding may directly limit the availability of some nutrients such as potassium through leaching or dilution (Jones and Etherington 1971, Jones 1975b). By changing the chemical species of nutrients to less bioavailable forms, introducing toxic forms of elements such as reduced iron or aluminum, or altering the pH of the environment, anoxic and reduced conditions associated with flooding may inhibit uptake of nutrients, such as phosphorus and nitrogen, by some plant species (Jones 1975b).

### *Biotic interactions*

Biotic factors also influence the distribution of nutrients in coastal ecosystems. In swales, decompositional release of nutrients is inhibited by anoxia during flooding, and nutrients are released in pulses whenever the soil dries out (Kushlan 1990, Conn and Day 1997). Plant–nitrogen-fixer symbioses, especially associations between shrubs of the genus *Morella* (*Myrica*) and the nitrogen-fixing actinomycete *Frankia*, alter the nitrogen content of the soil (Young et al. 1992, Young et al. 1994, Smith et al. 1995, Tolliver et al. 1997, Adler et al. 1998, Wijnholds and Young 2000). Besides adding nitrogen, leaf litter from *Morella* increases soil nutrients directly through decomposition and indirectly through increasing the cation exchange capacity of the soil (Young 1992, Smith et al. 1995, Adler et al. 1998).

There is evidence that vesicular-arbuscular mycorrhizae are important for the success of dune colonization and stabilization by grasses (Koske and Polson 1984). Moreover, mycorrhizal associations have been found important to the success and abundance of *Morella cerifera* and other dune species; this implies that mycorrhizae may play an important role in dune persistence as well (Semones and Young 1995, Field 1999, Perumal and Maun 1999). Soil moisture and nutrient availability affect mycorrhizal colonization in the dunes. These abiotic conditions may indirectly affect plant species abundances through facilitation of symbiotic relationships as well as directly through supplying nutritional requirements (Koske and Polson 1984, Al-Agely and Reeves 1995).

### *Community structure, succession, and state change*

The relation of plant assemblage composition to age along dune chronosequences in coastal and barrier island systems has been a major line of evidence for the existence



of ecological succession patterns (Cowles 1899, Levy 1990, Hayden et al. 1991, Avis and Lubke 1996, Kerley et al. 1996, McLachlan et al. 1996, Crawford and Young 1998a, Crawford and Young 1998b, Huggett 1998, Zonneveld 1999). Furthermore, much of the largely semantic argument surrounding the concept of plant succession and the climax community has involved studies of dune chronosequences (Clements 1936, Whittaker 1953, Olson 1958, Lichter 1998).

The serial succession of species replacements occurs rapidly on barrier islands because species there are adapted for rapid colonization in a dynamic physical environment (Ehrenfeld 1990, Levy 1990, Hayden et al. 1991, Hayden et al. 1995). Succession in the coastal marshes is determined by a complex interaction of abiotic stressors with interspecific competition and facilitation (Shumway and Bertness 1994, Brewer and Bertness 1996, Bertness and Leonard 1997, Hacker and Bertness 1999). For example, hypersalinity in newly created gaps in the marsh may favor salt-tolerant pioneering species, e.g. *Distichlis spicata* (Bertness and Ellison 1987, Bertness 1991a, Brewer and Bertness 1996, Brewer et al. 1998). Those species in turn ameliorate soil salinity and facilitate establishment of species that are otherwise superior competitors, e.g., *Spartina patens* (Bertness 1991b).

Establishment of a woody plant community on coastal dunes can happen fast enough (sometimes <10 yr) to allow researchers to actually observe successional processes rather than infer them (Ehrenfeld 1990, Johnson and Barbour 1990, Lichter 1998). In at least one North American coastal shrub species, *Iva frutescens*, there is an apparent positive feedback effect of adult plants creating better habitats for recruiting seedlings (Bertness and Yeh 1994, Hacker and Bertness 1995, Harley and Bertness

1996). Establishment of the climax-community maritime forest is not inevitable, however, and herb or shrub-dominated assemblages may persist indefinitely on some areas in response to disturbance regimes or other environmental conditions.

Frequent physical disturbances, such as storm overwash, as well as more gradual processes, like accretion and sedimentation or sea level rise, bring about ecological state changes in coastal areas like Virginia's barrier islands that not only are often more rapid than succession, but also can change its outcome (Hayden and Hayden 1994). For example, a severe storm overwash event on an island could, in a relatively short period of time, rearrange geomorphological features; alter nutrient cycling; change soil salinity and microbial communities; and rapidly replace a shrub-dominated community with a grass-dominated one.

Interspecific interactions, positive or negative, are also very important to plant succession and the composition of plant assemblages; this has been most closely studied in salt marsh systems (Bertness and Ellison 1987, Bertness 1991b, 1991a, Pennings and Callaway 1992, Bertness and Hacker 1994, Bertness and Yeh 1994, Shumway and Bertness 1994, Hacker and Bertness 1995, Shumway 1995, Brewer and Bertness 1996, Brewer et al. 1998, Hacker and Bertness 1999, Costa et al. 2003). Research is beginning to indicate that the coastal barrier landscape is a stress 'mosaic'. Nearly every area on a barrier island has a particular challenge: inundation and anoxia, high salt concentrations, low nutrient concentrations, droughty soils, etc. Although many species (an example from North America being *Spartina alterniflora* or *S. patens*) have a fairly broad environmental tolerance, their range is restricted by resource competition with other species (Bertness 1991b). Conversely, the distributions of other species (e.g., *Iva*

*frutescens*) seems to be contingent on positive interspecific interactions, such as soil amelioration (Bertness and Hacker 1994, Bertness and Yeh 1994, Hacker and Bertness 1995).

#### THE VIRGINIA COAST RESERVE LONG-TERM ECOLOGICAL RESEARCH SITE

##### *Site description*

I undertook this research on the barrier islands at the Virginia Coast Reserve Long-Term Ecological Research site, a multi-disciplinary, multi-institution ecological research site consisting of coastal areas off the Eastern Shore of Virginia (Callahan 1984, Franklin et al. 1990, Hayden et al. 1991, Olson et al. 1999). The Eastern Shore of Virginia forms the southeastern edge of the Delmarva Peninsula, which is the northeastern border of the Chesapeake Bay (Fig. 1). This region is situated on the coastal plain along the trailing edge of the North American Plate (Hayden et al. 1991). The seaside of the Delmarva Peninsula consists of a contiguous system of shallow bays (lagoons), tidal flats, oyster shoals, inlets, salt marshes, and barrier islands (Dueser 1990, Norcross and Hata 1990).

Virginia's barrier islands represent about 8% of North America's shoreline (Hayden et al. 1991) and are the last remaining undeveloped stretch of coastline on the mid-Atlantic seaboard (Badger and Kellam 1989, McCaffrey and Dueser 1990b). Located 3–20 km offshore, the islands are 2–14 km long, 1–2 km wide, and 1–9 m in elevation above mean sea level (Hayden et al. 1991). They are centered on latitude 37.50° north and longitude 75.66° west (McCaffrey and Dueser 1990a, 1990b). The tidal range is approximately 1 m, and average seaside wave heights range from 0.5–1.0 m (Hayden et al. 1991).

### *Research directives*

A primary hypothesis of the VCR LTER project is that ecosystem, landscape, and land-use patterns within terrestrial–marine watersheds are controlled by the vertical positions of the land, the sea, and the freshwater table surfaces. Sub-hypotheses pertinent to the barrier islands are 1) that dunes on the barrier islands are younger with proximity to the ocean, and successional processes along the dune chronosequence are responsible for biogeochemical variation across the landscape, 2) depth to the freshwater table and magnitude of storm disturbance determine species composition and successional processes, and 3) above and belowground productivity and decomposition rates are functions of depth to the freshwater table and nitrogen availability. Studies conducted there have, for example, focused on the roles of species life-history; probability of general disturbance; storm overwash effects, which include sand burial and flooding; and salinity tolerance from ground water or salt-spray (Schroeder et al. 1979, Fahrig 1990, Levy 1990, Hayden et al. 1995, Crawford and Young 1998a).

### *Barrier island plant species*

Although species composition varies among the islands, habitats and associated plant assemblages can be generalized for the islands. Characteristically, there are salt marshes on the lagoon side of the islands dominated by two growth forms of the halophytic grass *Spartina alterniflora* Loisel (Godfrey et al. 1979, McCaffrey and Dueser 1990a, McCaffrey and Dueser 1990b). Along lower dune slopes as well as the older swales, there are upland shrub thickets dominated by *Morella cerifera* (L.) Small, Myricaceae, along with *M. pennsylvanica* Loisel, *Baccharis halimifolia* L., and *Iva frutescens* L., both Asteraceae (Young et al. 1994, Young et al. 1995b, Crawford and Young 1998b). Tops of

dune ridges support various drought-tolerant grasses, such as *Spartina patens* (Aiton) Muhl., *Ammophila breviligulata* Fernald, *Aristida tuberculosa* Nuttall, or *Schizachyrium scoparium* (Michx.) Nash, and a few drought-tolerant forbs. Swale marshes predominantly contain the grasses *Spartina patens* and *Distichlis spicata* (L.) Greene; other graminoids, *Typha* spp., and dicots, such as *Hibiscus moscheutos* L. and *Phyla* (*Lippia*) *lanceolata* (Michx.) Greene, constitute a much smaller proportion of vegetation cover (Godfrey et al. 1979, pers. obs.). On dunes of the largest islands, there are forests composed mostly of loblolly pine, *Pinus taeda* L., with some dicot trees, e.g., *Persea borbonia* (L.) Sprengel, Lauraceae (McCaffrey and Dueser 1990a, pers. obs.). Red cedar, *Juniperus virginiana* L., Cupressaceae, is occasionally present both as a pioneer tree species on developing dunes as well as a secondary species on older dunes (Young et al. 1994, Martin and Young 1997).

#### THE PIMPLES OF THE VCR LTER

The habitats at the VCR LTER that were the focus of the current study are the ‘pimples’ of Hog and Parramore Islands. Pimples are dune landforms or mounds that superficially resemble other vegetation or tree islands found in other ecosystems. Vegetation islands and pimples are relatively small assemblages of woody or otherwise larger vegetation within a matrix of herbaceous species. Examples of tree islands can be found in alpine meadows and tundra, midland prairies, and wetlands like the Florida Everglades and Okefenokee Swamp (Rich 1934, Loveless 1959, Burbanck and Phillips 1983, Benedict 1984, Glasser 1985, Pauker and Seastedt 1996, Troxler Gann et al. 2005)

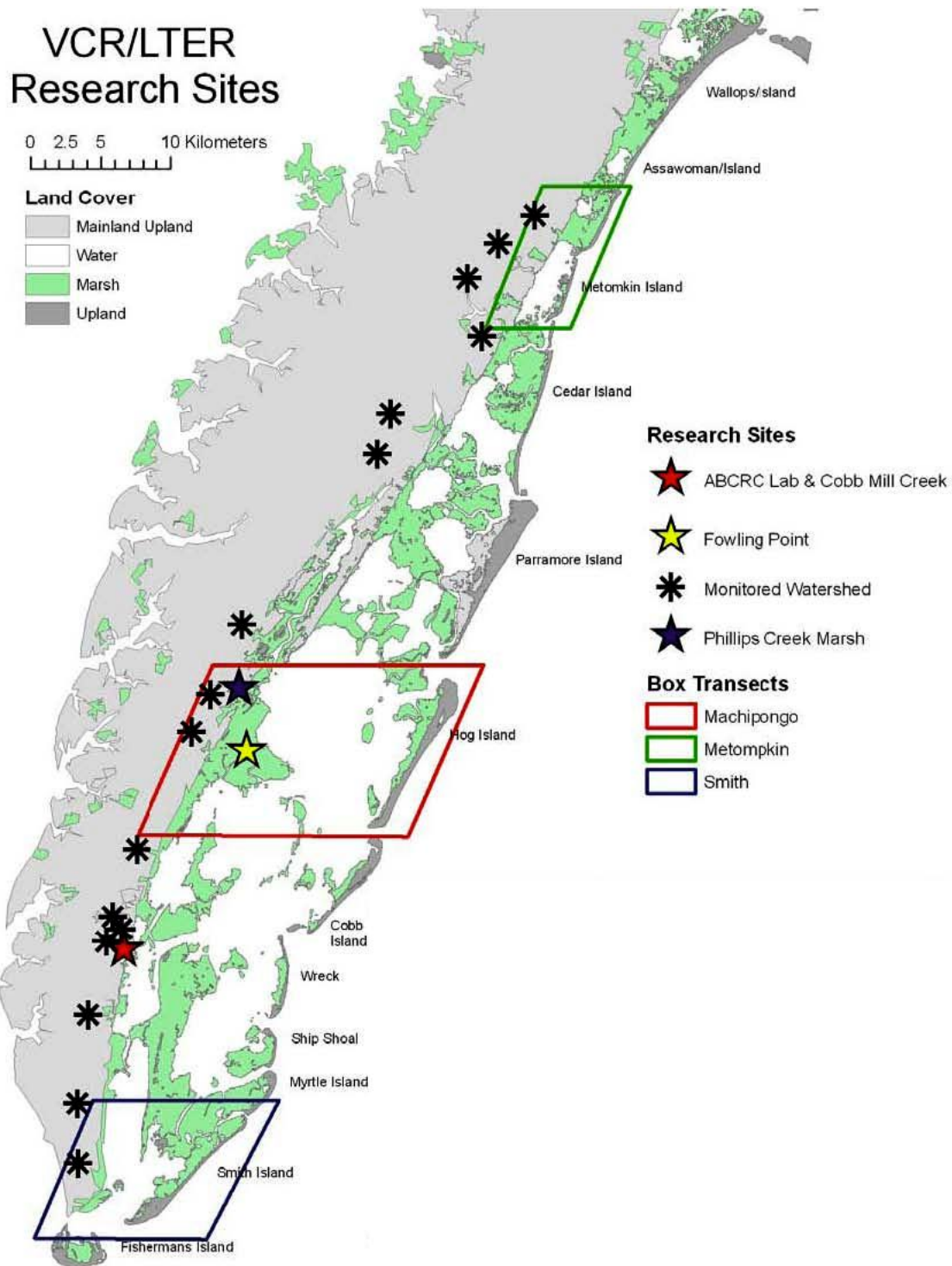


FIG. 1. Virginia's Eastern Shore and the VCR – LTER sites.

Nevertheless, most of these community patches originate from circumstances unique to their ecosystems. For example, tree islands in the Everglades arise from the filling of karst solution holes with peat, whereas tree islands in the Okefenokee establish on floating peat mats (Glasser 1985, Troxler Gann et al. 2005). Although there are vegetation islands in marshes, pimples on the barrier islands of Virginia are underlain by sand dunes, not peat, and so could not have arisen in either of those ways.

At the VCR, researchers first recognized and described pimple mounds on Parramore Island, but pimples occur on several other islands, including Hog Island, which is the most thoroughly studied of the chain (Rich 1934, Melton 1935, Dietz 1945, Cross 1964). As opposed to more typical crescent-shaped or parabolic dunes, pimples are circular to slightly ovate and flat-topped (Cross 1964, Anthonsen et al. 1996). Pimples are typically < 2 m taller than the elevation of the surrounding marsh; diameters range from 10 to 100 m (Fig. 2; pers. obs.). Geologists and ecologists have speculated that the pimples formed through various combinations and interactions of eolian deposition, vegetation stabilization, and overwash erosion. Nevertheless, there is no conclusive evidence of their actual origin (Rich 1934, Melton 1935, Dietz 1945, Cross 1964, Hayden et al. 1995).

Their elevation above mean high water level allows the accumulation of an underground freshwater lens floating on the saline groundwater (Hayden et al. 1995). This freshwater lens supports upland plant species on the shoulders of the pimple, but most pimples are too tall to support any but the most drought-tolerant species on their summits (Hayden et al. 1995).

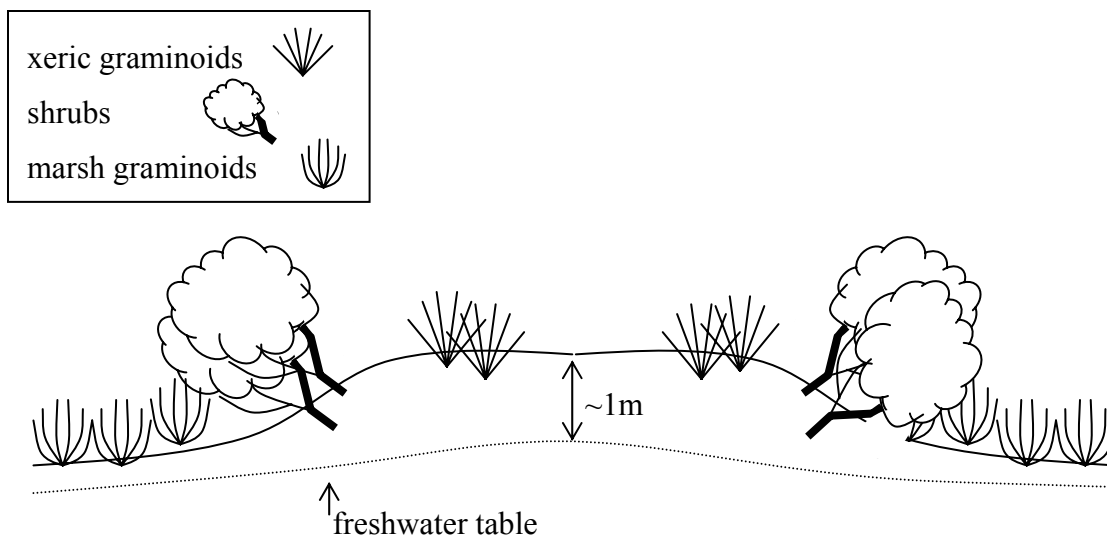


FIG. 2. Profile of a small pimple, not to scale; diameter varies from 10 to 20 m.

In aerial photographs of Parramore and Hog Island, pimples on both islands are concentrated on the eastern side of swales, which makes them appear associated with the younger, seaward dune ridge of the two ridges surrounding the swales. The largest concentration of pimples on Parramore is in a swale whose foredune was washed out by the Halloween or 'Perfect' Storm of 1991 (Young et al. 1995a). The lack of a foredune exposes the Parramore pimples to frequent overwash, which creates a brackish to saline marsh surrounding them (Hayden et al. 1995, Young et al. 1995a). Hog Island pimples, however, are found in interior, freshwater swales that are largely protected from overwash (Fahrig et al. 1993, Hayden et al. 1995, Young et al. 1995a). Parramore Island pimples appear to have a greater mean diameter than Hog Island pimples and seem to support richer and more diverse species assemblages. Some pimples on Parramore Island have a concentric pattern of alternating shrub and grass zones, which Hayden et al. (1995) hypothesized to reflect historical patterns of drought and rain events. No such patterning is readily observable on Hog Island pimples. Tree species richness appears greater on Parramore Island pimples than on Hog Island pimples.



Biological processes are probably more important than geological ones in the formation of pimples. There are what appear to be nascent pimples behind the youngest dunes on Hog Island. These have younger shrubs or only beach grasses on them but are similar in shape, size, and position (relative the main dune) as the interior pimples. This suggests that they may be dune fragments whose coalescence has been blocked by the deposition of newer dune. They persist because of stabilization by colonizing plants. The composition of colonizing plant species has a major role determining the 'mature' morphology of barrier island dunes (Godfrey et al. 1979, Ehrenfeld 1990, Levy 1990, Fahrig et al. 1993, Bailey et al. 1998). Because the VCR marks either the southern or northern boundary of several North American coastal plain plant species, it is floristically unique (Small 1933, Radford et al. 1968). This assemblage of plant (and perhaps mycorrhizal) species may mean that pimples are unique, endemic geologic phenomenon

Since they are rare geomorphologic features, the pimples of Virginia's barrier islands have interested geologists for years (Rich 1934, Melton 1935, Dietz 1945, Cross 1964). Biologists have studied them less. The only major attempt to study the ecology of pimples was when Hayden et al. (1995) initiated a groundwater displacement experiment to evaluate the role of hydrology in the community ecology of the Parramore pimples, but they were forced to abandon the project due to technical and logistical difficulties. It is important to study the plant assemblages on pimples and the environmental factors influencing them, not only because of the uniqueness of the pimples, but also to add to the understanding of upland plant ecology of the islands in general, since terrestrial systems in the VCR have received less attention than others. It is also unclear what differences in assemblage structure and dynamics may exist between pimples and the

main dune ridges of the islands. Pimples appear to be semi-isolated dune 'islands' within the islands, and this research will help to elucidate their similarities with the larger dunes so that they may be used as research units or natural mesocosms for researching upland ecology on barrier islands. Just as studying tree-fall gaps elucidates the dynamics of forest succession and regeneration, studying pimples can illustrate the ecology of the establishment and dynamics of the island system (Crawford and Young 1998a).

#### RESEARCH GOALS AND HYPOTHESES

My main hypotheses for this study were 1) that freshwater availability is the primary factor determining assemblage structure on pimples and 2) that pimple size influences the diversity of species assemblages. Research goals for testing my hypotheses were 1) to describe the plant assemblages associated with pimples on Hog Island and Parramore Island, 2) to relate the edaphic and geomorphological characteristics of the pimples to the species composition of plant assemblages on them at island-level, pimple-level, and sub-pimple-level scales, and 3) to compare assemblage – environment interactions on pimples and main dune ridges. Accomplishing these goals entailed field vegetation surveys of a representative sample of pimple and dune plant assemblages and environmental monitoring.

Field measurements of assemblage structure were coupled with observations of abiotic conditions, such as total C & N, pH, salinity, elevation, freshwater table depth and fluctuation, and probability of storm overwash. Multivariate statistical techniques were used to describe the relative importance of these factors to assemblage characteristics: species diversity and richness, and the presence of certain species indicative of the

various assemblages. Studying pimple community dynamics on more than one island was intended to increase the generality of inferences drawn from the study.

Based on the hypotheses of the VCR LTER project, a primary assumption of this study was that the depth to freshwater and elevation would be the most important factors determining plant assemblage structure on the pimples. It was more difficult to predict other environmental factors contributing to variation in assemblage structure. Available soil nitrogen would surely influence density, if not composition, of species on pimples. Another prediction was that presence and density of the nitrogen-fixing shrub *Morella cerifera* would affect species composition through modifying soil nitrogen content (Smith et al. 1995). Between-island differences in species composition would be influenced by water quality in the surrounding marsh, i.e., water conditions in the marsh would affect pore water salinity and redox potential on pimples. Between-island differences could also be explained by rate of disturbance, but estimates of storm overwash potential have only been calculated for Hog Island (Kochel and Wampfler 1989, Fahrig et al. 1993, Hayden et al. 1995). Species interactions were likely to be important, but their evaluation was outside the scope of this study.

## CHAPTER 2

### EXPERIMENTAL DESIGN AND METHODOLOGY

#### INTRODUCTION

An overarching hypothesis of the VCR LTER project is that relative elevations of land, sea, and freshwater table are expected to drive ecological processes. Furthermore species composition on pimples appeared to change relative to land elevation on a sub-meter scale. Because of those two factors, accounting for elevation in the sampling scheme was important. Rather than sampling species along an elevation gradient, it was more appropriate to limit sampling units to roughly the same elevation on the pimple. That fact combined with the density of the shrub thickets on the pimples and the apparent narrowness of vegetation zones provided cogent reasons for choosing a linear sampling method instead of a quadrat or other two-dimensional technique. I tested two linear sampling techniques: line-intercept and point-intercept (described below), for their efficacy and statistical power in measuring species relative cover or density along the same elevation (Godfrey et al. 1979, Bonham 1989, Dale 1999).

#### PILOT STUDY

Pilot sampling of species and tests of the two sampling technique occurred on three Hog Island pimples in June–July 2002. Each sampling unit was a 5 m linear transect marked with measuring tape and oriented parallel to the elevation contour of the pimple. Transect placement was stratified along the elevation gradient; there were three transects in each of four surveyed quadrants, which faced the cardinal directions, i.e., 12 transects per pimple. Relative cover for each species was recorded for each transect using both the point-intercept method, in which species contacting a rod or plum line at 50 random points along a transect are recorded as well as the line-intercept method, in which linear

distances of plant coverage are recorded. For the first method, abundances would be recorded as number of encounters, and for the second abundance would be recorded as cm of coverage by each species. There were two sampling strata recorded for each method: plant species less than one m tall belonged to the understory and woody species above one m were in the shrub layer or overstory. I evaluated each method for ease and expedience, compared results from each method, and used the point-intercept data to estimate the number of point intercepts needed to confidently sample within 10% of the true mean (Dale 1999).

In the field, the point-intercept method was more efficient than line-intercept measurements because it reduced the total number of observations made per transect. Paired t-tests determined if the percent cover values for species in transects differed between the two sampling methods. Species cover recorded with the line-intercept method did not differ from species cover recorded at 50 points along a transect ( $p = 0.96$ ). Furthermore, both random and stratified sub-samples of the point-intercept data did not significantly differ from the original line-intercept data for sub samples containing at least 10 of the original points ( $p = 0.74\text{--}0.98$ ), suggesting that fewer points could be used without sacrificing accuracy. Nevertheless, computing sample size estimation for the point-intercept data revealed that  $> 100$  points/transect would be required to sample consistently within a 10 % confidence interval around the true mean (Bonham 1989). In other words, statistical power would be lost with the more efficient sampling method. Conversely, the line-intercept method provides the actual species abundances rather than a sub-sampled mean and is not subject to concerns about statistical power.

During field trials in summer 2002 and 2003, a twelve-transect sampling array proved prohibitively time-consuming for floristic surveys; i.e., it would not be possible to finish an entire survey of all sites before growing conditions changed. Instead of twelve transects, I decided to use a three-transect array.

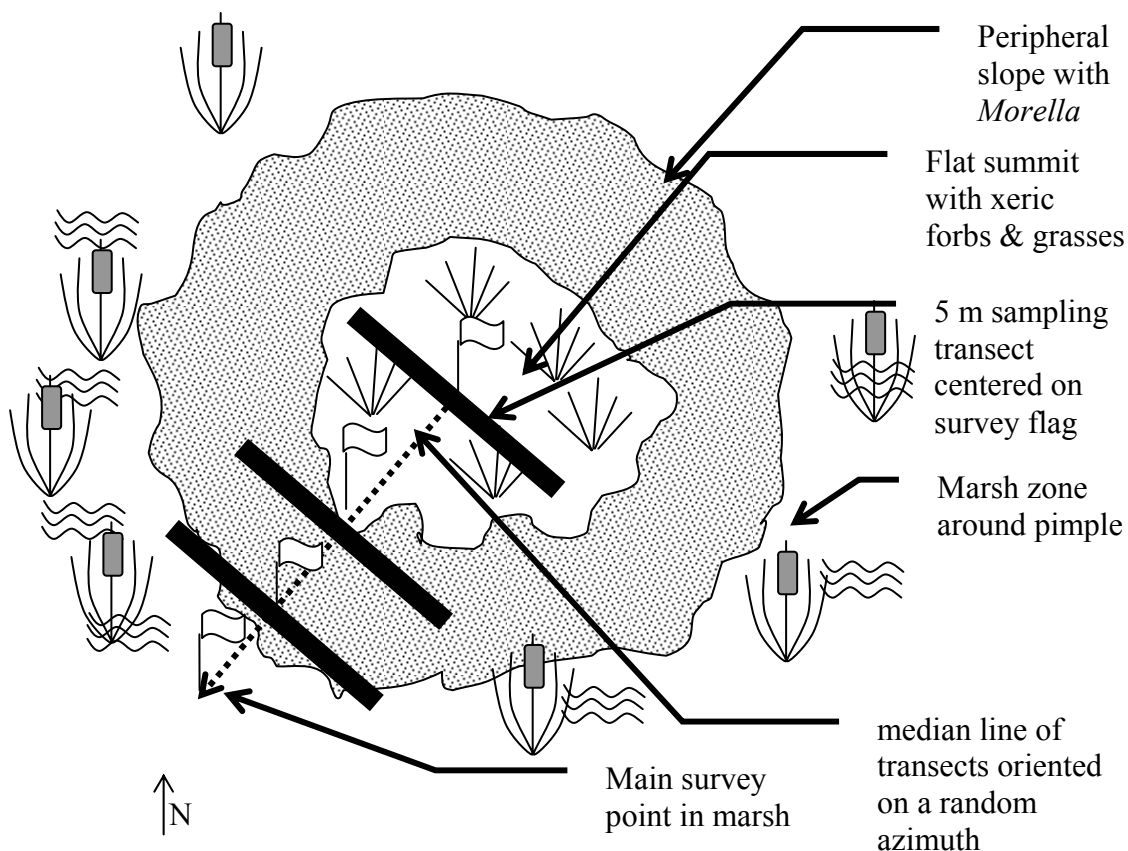


FIG. 3. Sampling method.

#### FINAL SAMPLING CONFIGURATION

To establish a sampling array, I randomly located a survey point outside of a pimple. Using an electronic transit (Pentax Total Station laser theodolite), I surveyed three more transect center points in a straight line connecting the center of the pimple with the survey point (FIG. 3). I stratified placement of center points by elevation. The

first transect was in marsh at the periphery of shrubs; the second transect was on the slope of the pimple sides under shrubs; and the central transect was placed outside the shrub zone in the pimple summit. It was not feasible or practical to survey elevation waypoints on Hog Island in order to calculate true elevation above sea level; therefore the relative elevation of each transect above marsh ground level, i.e., the surface of the muck layer underneath the detritus or water, was recorded. The relative distances from the origin point and the relative elevations allowed simple trigonometric calculation of slope at each transect. Using GPS coordinates of the origin survey point and the transect center in the pimple interior allowed a fairly accurate calculation of the azimuth (aspect) of the transect array. Array installation on Parramore Island pimples differed from the above methods in that a tripod-mounted laser level and stadia were used instead of the automatic transit.

Permanent transects were established during summer 2003 for Hog Island pimples and summer 2005 for Parramore Island pimples. Pimples on Hog Island lie along a nearly North – South line in the oldest interior swale marsh between ridges that date from 1871 and 1955; most lie closer to the 1955 ridge. Seventeen pimples were chosen randomly from a ca. 700 m section of that line centered on the vehicle trail (Fig. 4). Pimples on Parramore Island are in the southernmost half of the island, an area fronted on the lagoon side of the island by a ~ ½ km wide strip of soft-bottom salt marsh and tidal creeks that are too shallow for motorized boats at low tides. This made reaching pimples on Parramore impractical and potentially dangerous for most of the study. Four pimples studied on Parramore Island were chosen based on accessibility from the Swash, a channel through the marsh, and were roughly in a southwest–northeast line connecting

442641 E, 4151840 N and 443060 E, 4152222 N (UTM zone 18, WGS84 datum; latitude – longitude equivalent is 37.512° N, 75.649° W to 37.515° N, 75.654° W).

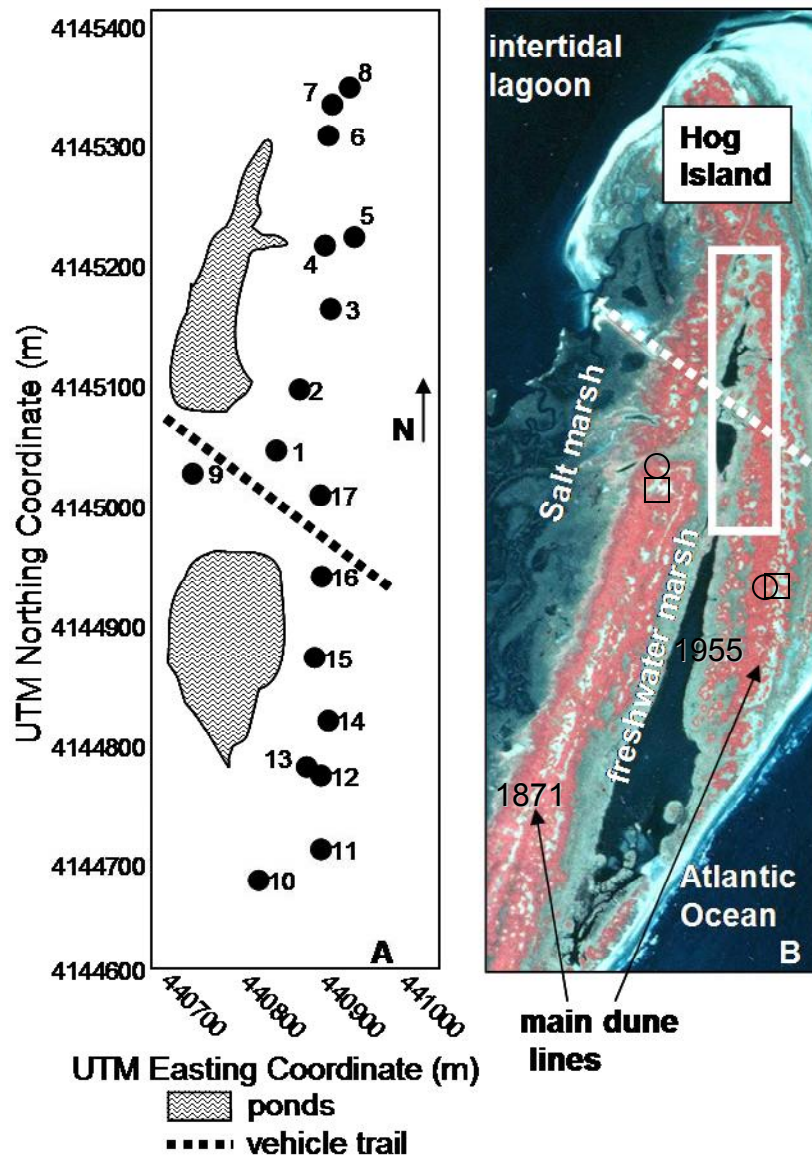


FIG. 4. Map and aerial photograph of pimples and main dunes sampled on Hog Island. The area represented by the graphical map (A) is denoted by the rectangle on the aerial photograph (B). Open circles and squares in B respectively represent the location of the long-term swale and dune water table-monitoring wells. Coordinates are for UTM zone 18 using the WGS84 datum. The northwest and southeast corners of the map (A) are 75.670°W, 37.454°N and 75.667°W, 37.446°N, respectively.



During the same period that the pimple transects were being established on Hog Island, I established ten more transects near two water-recording wells, S4 and S3, which are located in swales associated with the oldest and second-oldest dune ridges on the island, respectively (Conn and Day 1993, 1997, Dilustro and Day 1997, Day et al. 2001). Not only are these wells of known elevation, they also provided water level data for transects. Five more transects were set up near wells D3 and D4, which were located on dunes near the swale wells. In addition to data from those transects, species data were included from control plots used for a long-term nutrient addition study located in the dunes around the wells (Stevenson and Day 1996, Conn and Day 1997, Day et al. 2001).

#### SPECIES COLLECTION

At the start of the study, I began collecting voucher specimens for species encountered on and around the pimples of Hog Island and eventually all new species, including ferns and mosses, and a few unique species from Parramore Island. The specimens were identified and deposited at the Old Dominion University Herbarium.

## CHAPTER 3

### PLANT ASSEMBLAGE STRUCTURE AND DIVERSITY PATTERNS

#### INTRODUCTION

The basic goal of community ecology is to describe the interrelationships, social structures, and environmental interactions of the species and habitats within a specified region (Cowles 1899, Clements 1936, Whittaker 1956, 1960, Magurran 1988, Bonham 1989, Fauth et al. 1996, Morin 1999). Some of the earliest studies of biodiversity were in dune plant assemblages (Cowles 1899, Clements 1936, Magurran 1988). Investigations of dune and barrier island ecology are still relevant today because they advance knowledge about general ecological theories and concepts like succession and island biogeography. Understanding barrier islands also has practical implications for dune restoration, wetland mitigation, and wildlife management (Hosier and Eaton 1980, Ehrenfeld 1990, Johnson and Barbour 1990, Hayden et al. 1995, Erwin 1996).

Because dunes are frequently disturbed, the species composition of plant assemblages on them can change significantly in short time spans and ‘climax’ communities are either unattainable or unstable (Ehrenfeld 1990, Young et al. 1994). Studying the rapid species turnovers and system state changes may help ecologists understand less dynamic or more slowly-changing ecosystems (Belsky and Amundson 1986, Ehrenfeld 1990, de Castro 1995, Anthonsen et al. 1996, Day et al. 2001). This may especially be true for learning about the impact of edaphic and geomorphological factors on the sequence of succession such as alterations in dune stability, height, disturbance frequency, and soil amendments (both biotic and abiotic) (Fahrig et al. 1993, Young et al. 1994, Young et al. 1995a, Young et al. 1995b).

Island biogeography and the species – area relationship are basic concepts in ecology (Gleason 1925, MacArthur et al. 1966, Connor and McCoy 1979). Nevertheless, theories concerning relationships of isolation and habitat area to species richness and diversity are still being developed and refined (Crist and Veech 2006). Barrier islands and dune communities are well-suited to investigations on those topics because they are both ecosystems of varying size and isolation.

Because most of the world's population lives in coastal areas, understanding coastal and dune ecosystems often has demonstrable, practical value in terms of protecting coastal resources and real estate (Brinson 1996). Describing patterns of plant diversity on dunes helps to advance knowledge about 'healthy' dune ecosystems and remains important to the study of ecology (Clayton 1972, Christian et al. 1998). Virginia's barrier islands are excellent research subjects in this regard because they represent some of the most pristine and most extensive coastal habitat on the US Atlantic seaboard.

In this chapter, I describe the assemblage structure of pimples on Hog and Parramore Islands using traditional density descriptors, three different ordination methods, an assortment of diversity indices, and parametric tests. My intentions were to provide a comprehensive study of the plant species on pimples and compare the usefulness of some 'traditional' and newer techniques, with special emphasis on the application of ordination and diversity indices.

#### *General descriptors of assemblage structure*

Basic mathematical methods used in describing patterns in communities include species frequency, dominance, and importance; species–area curves; species

accumulation curves and rarefaction curves; and diversity indices (Curtis and McIntosh 1951, Dawson 1951, Whittaker 1960, McIntosh 1962, Bannister 1966, Will-Wolf 1980, Magurran 1988, Palmer 2007). More elaborate methods that are becoming increasingly popular since the advent of inexpensive computing power are ordination methods like non-metric multidimensional scaling (Palmer 2007).

Besides species richness, which is the number of species, other basic descriptors of assemblages are frequency, density, dominance, relative frequency, relative density, relative dominance, and importance values (Curtis and McIntosh 1951, McIntosh 1962, Bannister 1966, Will-Wolf 1980). These measures are good tools for a preliminary overview of plant census data because they give an indication of the relative abundance of a particular species. Nevertheless, relationships between species must be inferred, and it is difficult to use importance values to reach an overarching assessment of assemblage dynamics.

#### *Rarefaction curves*

Rarefaction curves are estimates of the cumulative number of species found as a function of either the number of individuals sampled or the number of samples taken (Olszewski 2004, Crist and Veech 2006). They allow interpolated estimates of total species richness in a sample area and comparison of richness between two assemblages that have not been sampled equally (Chao 1987, 1989, Colwell and Coddington 1994, Lee and Chao 1994, Peterson and Slade 1998, Colwell et al. 2004, Olszewski 2004, Crist and Veech 2006). This feature was important to me, since I was comparing pimple transects with long-term transects that had been censused with different methods (Day et al. 2001). Rarefaction curves also can be used to estimate sampling adequacy, species

diversity indices, and diversity partitions, when diversity is measured as species richness (Chao 1987, Lee and Chao 1994, Chazdon et al. 1998, Crist et al. 2003). See the discussion of diversity partitioning below.

### *Ordination*

Ordination techniques are statistical methods usually employing sample averages and matrix algebra, and most can be thought of as special adaptations of the general linear model (Dawson 1951, Bray and Curtis 1957, Swan 1970, Gauch and Whittaker 1972b, Gauch 1973, Hill 1973b, Gauch et al. 1977, Gauch 1982b, Kent and Ballard 1988, Crist et al. 2003, Palmer 2007). Their purpose is to reduce the number of dimensions in multidimensional relationships by determining correlations among a set of research objects and putting them in order along explanatory axes. (Bray and Curtis 1957, Bannister 1966, Gauch and Whittaker 1972b, Gauch 1973, Gauch et al. 1977, Gauch 1982b, Kent and Ballard 1988, Clarke 1993, Palmer 2007). When plotted against two or three explanatory axes, positions of research objects in the resulting ‘ordination’ space reveals their relative similarity or dissimilarity (Palmer 2007). In theory, these patterns are the result of species’ responses to environmental variation and interactions.

I had a choice of several ordination techniques that have risen and fallen in popularity among different groups of ecologists over the years (Whittaker 1956, Bray and Curtis 1957, Swan 1970, Walker and Wehrhahn 1971, Gauch and Whittaker 1972b, Gauch 1973, Gauch and Chase 1974, Gauch et al. 1977, Peet and Loucks 1977, Orłóci 1978, Gauch and Stone 1979, Gauch 1982b, Pielou 1984, ter Braak and Barendregt 1985, ter Braak 1986, Peet et al. 1988, Trejo-Torres and Ackerman 2002). While most researchers agree that they should carefully choose the technique most appropriate to

their study, few agree on the circumstances under which a technique is appropriate (Pielou 1984, Kent and Ballard 1988). I followed the example of other researchers and evaluate the usefulness of a selection of techniques, rather than one, in describing pimple assemblage structure (Wentworth 1981, Westman 1981, Chang and Gauch 1986). I used two well-established techniques, Bray-Curtis ordination and principal components analysis, and a more modern and computationally intensive method, non-metric multidimensional scaling (Goodall 1954, Bray and Curtis 1957, McCune and Mefford 1999, Palmer 2007).

#### *Diversity indices and diversity partitioning*

Among all the ways to describe assemblage structure, biological diversity has been a perennial theme of community ecology (Cowles 1899, Whittaker 1956, Bray and Curtis 1957, Hill 1973a, Magurran 1988, Tilman 1997, Peltzer et al. 1998, Chiarucci et al. 2001). Ecologists and environmentalists consider biological diversity to have intrinsic value and to relate directly to ecosystem integrity (Magurran 1988, Colinvaux 1993, Booth and Grime 2003). Researchers have been developing and refining mathematical and field techniques for estimating diversity for a century or more (Cowles 1899, Gleason 1925, Bray and Curtis 1957, Gauch 1973, 1982a, Pielou 1984, Bonham 1989, Giannini 2003). Studying the diversity of assemblages on isolated geomorphological features like pimple dunes presented a good opportunity to advance knowledge on this topic.

The three most common measures of species diversity are species richness ( $S$ ), Shannon's diversity index ( $H$ ), and Simpson's diversity index ( $D$ ). Both the Shannon and Simpson's indices take into account species richness as well as species evenness. I used both indices because they are well-known and easy to calculate and interpret.

*Partitioning diversity.* I wanted to look for differences in assemblage structure between habitat types (marsh, shrubs, and summits), between pimples and main dunes, between islands, and among seasons. Fortunately, there are many theories and methods for determining diversity at different spatial (and temporal) scales. A predominant view first proposed by Whittaker (1966) is that diversity across a landscape can be broken into at least three partitions: site-level diversity ( $\alpha$ -diversity), the diversity that represents the change in species between sites ( $\beta$ -diversity), and the total diversity of all sites in a landscape ( $\gamma$ -diversity). Although some have found problems with this approach, e.g., defining the sizes of site and landscape, it has proven to be a useful concept with many proposed methods of measurement (Whittaker 1960, Gauch and Whittaker 1972a, Alatalo and Alatalo 1977, Shmida and Wilson 1985, Lande 1996, Whittaker et al. 2001, Veech et al. 2002, Booth and Grime 2003, Summerville and Crist 2005, Crist and Veech 2006).

A problem with the partition concept of diversity is lack of comparability. Whereas  $\alpha$ - and  $\gamma$ -diversity are usually measured as richness or with a diversity index,  $\beta$ -diversity is usually measured with any number of indices that are specific to it (Shmida and Wilson 1985, Magurran 1988, Olszewski 2004). Although the utility of  $\beta$ -diversity indices has been established (Shmida and Wilson 1985, Magurran 1988), they cannot be directly compared to indices used to measure  $\alpha$ - and  $\gamma$ -diversity. Without direct comparability among all levels, the hierarchical partition concept is less useful. I decided it would be instructive to calculate a few direct measures of  $\beta$ -diversity, but wanted to find a method for measuring diversity that would be comparable at all scales:  $\alpha$ ,  $\beta$ , and  $\gamma$ .

*Additive partitions.* A recent advance in measuring partitions of diversity was well-suited to the needs of my study. This development is the concept of Whittaker's

partitions being additive, instead of multiplicative as he first proposed (Lande 1996, Veech et al. 2002, Crist and Veech 2006). Within this framework, diversity partitions at each level are additive, such that the mean diversity within samples ( $\alpha$ ) plus the mean diversity among samples ( $\beta$ ) equals the total system diversity ( $\gamma$ ), regardless of the statistic used to define diversity (Veech et al. 2002, Crist and Veech 2006). Furthermore, there can be any number of hierarchical partitions of diversity based on scale, i.e., multiple  $\alpha$  and  $\beta$  levels (Crist and Veech 2006). It has also been suggested that hierarchical levels of diversity can include temporal levels as well as spatial ones (Summerville and Crist 2002, Crist et al. 2003, Summerville and Crist 2005). I used methods based on these theories to measure diversity at the transect, pimple, and season level. There have not been many comprehensive studies of additive diversity partitions at different spatial and temporal scales and at present none have been conducted in barrier island or dune systems.

*Rarefaction curves.* Rarefaction curves (see above) also have use for determining diversity partitions when diversity is measured as species richness. The last point on a curve is  $S_{\text{obs}}$  or  $\gamma$ -level richness (Summerville and Crist 2002, Veech et al. 2002, Crist et al. 2003, Summerville and Crist 2005, Crist and Veech 2006, Summerville et al. 2006). Using rarefaction curves for estimating diversity partitions is informative because it provides a graphical representation of the partitions.

### *Study goals*

The principle goals of the current study were: 1) define assemblage groups on different pimples, 2) estimate the total number of species on the pimples, 3) look for evidence of succession in temporal variation, and 4) determine significance in spatial



patterns of diversity at different scales. My goal for examining spatial patterns was to find A) a relationship between distance and similarity in pairwise comparison of pimples, B) a discernible spatial relationship among species within pimples, and C) significant differences in diversity at the transect, pimple, and island level, i.e.,  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversity (Whittaker 1960, Gauch and Whittaker 1972a, Peterson and Slade 1998, Gotelli 2001, Crist and Veech 2006). Where possible and practical, I evaluated more than one approach to each of these questions for the sake of comparison.

#### MATERIALS AND METHODS

Field methods are described in Chapter 2. I used pivot tables in Microsoft Excel to calculate the sum of species measurements within each transect. The spatial distribution of species within transects is therefore not represented in my analyses.

##### *General descriptors*

*Species richness, diversity indices, and parametric tests.* In addition to recording species richness, I calculated Shannon and Simpson's diversity indices at the transect-, pimple-, and whole-island level. Both indices account for species richness and species evenness by using the proportions ( $p_i$ ) of total abundance represented by each species in their calculation (Table 1). Conventionally,  $p_i$  is calculated as the number of individuals of species  $i$  divided by the total number of individuals for all species in the sample. The range of values for the Shannon index varies relative to  $S$  (Hill 1973a, Magurran 1988, Crist et al. 2003, Crist and Veech 2006). The term 'Simpson's index' has been applied to three different calculations: Simpson's index, Simpson's index of diversity, and Simpson's reciprocal index. Both of the first two measures produce values in the range of 0–1, but in the first index diversity is high as values approach zero; the opposite is true

for the second index. Values for the reciprocal index vary  $1-S$ . The second index has the advantages of having the same range of outcomes regardless of  $S$  and being intuitively interpreted, i.e., diversity increases as values increase. Simpson's index of diversity is therefore the index used in my analyses (Hill 1973a).

TABLE 1. Calculation of Shannon and Simpson's diversity indices (Hill 1973a, Crist and Veech 2006).

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Variables:

$H$  = Shannon diversity index  
 $D_x$  = different variations on Simpson's index  
 $S$  = species richness in sample  
 $p_i$  = proportion of the abundance of the  $i$ th species relative to the total abundance of all species; e.g., (# individuals of species  $i$ )/(total # individuals).

Formulas:

Shannon index	$H = - \sum_{i=1}^S p_i \ln p_i$
Simpson's index, proper	$D_1 = \sum_{i=1}^S p_i^2$
Simpson's index of diversity	$D_2 = 1 - \sum_{i=1}^S p_i^2$
Simpson's reciprocal index	$D_3 = \frac{1}{\sum_{i=1}^S p_i^2}$

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I used ANOVA to test hypotheses that species richness and species diversity varied at both transect and pimple level based on habitat type and year. For each test of richness, Shannon diversity, and Simpson's diversity, I used a main effects model with year, habitat, pimple, and transect as terms. Full-factorial models did not allow enough degrees of freedom for a test to be performed. I performed multiple comparisons with Tukey's test. I considered  $P \leq 0.05$  significant for both ANOVAs and multiple comparisons. When the outcome would be biased by an incomplete dataset, I excluded

2005 data from calculation of annual means and most ANOVAs. I also calculated means for species abundance data from the long term study on the main dunes as a point of comparison.

*Importance values.* Individual counts allow more options with diversity analyses and other descriptors than continuous measures of species abundance, such as % cover. Nevertheless, I did not attempt to count individual ramets because the majority of species were clonal and any individual count would have been artificial and prone to bias. An example of problems arising from this situation involves the calculation of importance values (IVs) for species (Table 2).

TABLE 2. Species abundance measures used in calculating species importance values (Curtis and McIntosh 1951, McIntosh 1962, Bannister 1966, Will-Wolf 1980).

Measurement	calculation
Species frequency	$\frac{\text{number of plots in which a species is found}}{\text{total number of plots surveyed}}$
Species density	$\frac{\text{number of individuals found for a species in all plots}}{\text{total area (or other measure of sampling effort) surveyed}}$
Species dominance	$\frac{\text{total coverage recorded for a species}}{\text{total area or distance surveyed (i.e. total potential coverage)}}$
Relative frequency	$\frac{\text{frequency for a given species}}{\text{sum of all species frequencies}}$
Relative density	$\frac{\text{density for a given species}}{\text{sum of all species densities}}$
Relative dominance	$\frac{\text{dominance for a given species}}{\text{sum of all species dominance values}}$
Importance Value	relative frequency + relative density + relative dominance

I calculated a yearly average of dominance, relative dominance, frequency, and relative frequency for each species, but, without counts of individuals, I could not calculate density or relative density. As an alternative, I included  $IV_{\text{mod}}$  (my designation) for species, which is the sum of relative dominance and relative frequency.

### *Rarefaction curves*

Calculation of the expected outcome curves can be accomplished both by simulation and with analytical formulas, the most common being Mao's tau,  $\tau$  (Table 3) (Chao 1987, 1989, Lee and Chao 1994, Chazdon et al. 1998, Olszewski 2004). I used the EstimateS 8.0 program to produce rarefaction curves, Mao's tau values, and the two rarefaction-curve species richness indicators used in my analyses: Chao 2 and incidence-based coverage estimator (ICE) (Colwell et al. 2004, Crist and Veech 2006). These estimators use the incidence of rare species and the total observed species richness ( $S_{\text{obs}}$ ) to predict the actual  $S$  (Chao 1987, Lee and Chao 1994, Chazdon et al. 1998, Crist et al. 2003). By determining if the curve has reached an asymptote or by comparing  $S_{\text{obs}}$  to a richness estimator, one can assess how successful field sampling was in capturing all species present. Confidence intervals for the range of likely total richness values can also be calculated, and Mao's tau can also be used to predict confidence intervals along the entire curve as per Colwell et al. (2004). I also used rarefaction curves to estimate diversity partitions (see below).

TABLE 3. Formulas for species richness estimators that approximate rarefaction curves. The different sources of these formulas in part used the same letters for different variables. Throughout the dissertation, I changed variable designations from the originals to avoid confusion and maintain continuity (Chao 1989, Chazdon et al. 1998, Crist et al. 2003, Crist and Veech 2006).

Variables:

$S_{obs}$  = observed species richness for entire study

$S_k$  = the number of species found in exactly  $k$  samples (transects); e.g.  $S_1$  is the number of species in one sample,  $S_2$  is the number of species in two samples, etc.

$S_{Chao2}$  = Chao2 true richness estimator

$S_{ice}$  = incidence-based coverage estimator of true species richness

$S_{freq}$  = number of species found in  $> 10$  samples, transects, or quadrats

$S_{infr}$  = number of species found in  $\leq 10$  samples, transects, or quadrats

$B$  = the total number of samples (transects)

$b$  = the number of samples in a subset;  $b = 1, 2, 3 \dots B$

$Q_k$  = number of species that occur in  $k$  samples, transects, or quadrats; e.g.,  $Q_1$  = the number of species found in only one sample

$\gamma_{ice}$  = estimated coefficient of variation for  $Q_k$  of infrequent species (Chazdon et al. 1998)

$C_{ice}$  = sample incidence coverage estimator (Chazdon et al. 1998)

$\tau(b)$  = Mao's tau unbiased estimator of species richness in  $b$  samples

$\xi$  = a combinatorial coefficient used in the calculation of  $\tau(b)$

$\sigma$  = a variance estimator for calculating the confidence interval of  $\tau(b)$

$\tilde{S}$  = unknown species richness used in calculating the confidence interval of  $\tau(b)$

Formulas:

Total observed richness: 
$$S_{obs} = \sum_{k=1}^B S_k$$

Chao2: 
$$S_{Chao2} = S_{obs} + \frac{Q_1^2}{2Q_2}$$

ICE: 
$$S_{ice} = S_{freq} + \frac{S_{infr} + Q_1 \gamma_{ice}^2}{C_{ice}}$$

Mao tau rarefaction estimator: 
$$\tau(b) = \sum_{k=1}^B (1 - \xi_{kb}) S_k = S_{obs} - \sum_{k=1}^B \xi_{kb} S_k$$

where 
$$\xi_{kb} = \begin{cases} \frac{(B-b)!(B-k)!}{(B-b-k)!B!} & | (k+b \leq B) \\ 0 & | (k+b > B) \end{cases}$$

note that when  $b = B$ ,  $\xi = 0$ ; therefore  $\tau(B) = S_{obs}$

(Table 3, continued)

Mao tau confidence intervals, i.e.,  $\tau(b) \pm 1.96\sigma(b)$ :

$$\sigma^2(b) = \sum_{k=1}^B (1 - \xi_{kb})^2 S_k - \tau^2(b) / \tilde{S}$$

$$\text{where } \tilde{S} = S_{obs} + \frac{(B-1)S_1^2}{2BS_2}$$


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### *Ordinations*

To describe communities with respect to species and habitat associations I used multivariate ordination tests: Bray-Curtis ordination, non-metric multi-dimensional scaling, and principal components analysis. I performed all analyses with PC-ORD v. 4; the NMS analysis was preceded by an ‘autopilot’ analysis to determine the best number of axes to ordinate the result. Pearson’s r correlation coefficient was used to judge the variables most important to determining axes.

### *Resampling and diversity partitions*

To examine the spatial partitioning of diversity and to determine if diversity changed between years in each pimple, I used resampling simulations (PARTITION program). I compared diversity partitioning between pimples and the main dunes and compared those results with direct calculations of different indices of  $\alpha$ -level (transect) and  $\beta$ -level (turnover between transects) species diversity (Magurran 1988, Crist and Veech 2006).

I used sample-based randomizations to calculate diversity partitions rather than individual-based randomization. Because sample-based randomization “preserves the

patterns of intraspecific aggregation in the observed data, it is most useful in testing explanations of species diversity that are based on nonrandom species assemblages” (Crist et al. 2003). To perform a sample-based randomization analysis of diversity partitions, values from observed samples at level  $h$  are randomly allocated to the larger sample units at level  $h + 1$  that all belong to the same even larger sample unit at level  $h + 2$ . This process is repeated 1,000 – 10,000 times, typically, to create a bank of null-value data sets, i.e., diversity values that would occur if samples were randomly distributed within each sampling level. The proportion of null values that exceeds a particular observed value then becomes the probability (P-value) that a greater value than the observed would occur by chance. Thus, very high probabilities ( $P \geq 0.95$ ) indicate that observed values were considerably less than random values and should be considered statistically significant in addition to those probabilities  $\leq 0.05$ .

I used three different indices of  $\beta$ -diversity (Table 4). Whittaker’s measure of  $\beta$ -diversity relies on the ratio of total species richness to average sample richness (Whittaker 1960). Cody’s measure uses species turnover between sites (Magurran 1988). Wilson and Shmida’s measure combines Whittaker’s with Cody’s (Wilson and Shmida 1984, Shmida and Wilson 1985, Magurran 1988).

Direct measurements of diversity partitions were made using the concept that partitions are additive. Consider, for example, a hypothetical case with four partitions of diversity: the average  $\alpha$ -level diversity in each transect, the average  $\beta_1$ -level between transects, the average  $\beta_2$ -level between plots, and the overall diversity ( $\gamma$ ). In that case,  $\alpha_1 + \beta_1 = \beta_2$  and  $\alpha_1 + \beta_1 + \beta_2 = \gamma$  (Table 5); this is true if diversity is measured as species richness (intuitive), or with either Shannon’s or Simpson’s diversity index (perhaps not as

intuitive; Crist and Veech 2006). Theoretical ecologists have devised methods to capitalize on the additive property of diversity partitions and calculate  $\alpha$ - and  $\gamma$ -diversity so that  $\beta$ -diversity levels can be determined as the difference between them (Table 5) (Whittaker 1960, Gauch and Whittaker 1972a, Magurran 1988, Colwell and Coddington 1994, Lande 1996, Chazdon et al. 1998, Peterson and Slade 1998, Gotelli 2001, Longino et al. 2002, Veech et al. 2002, Colwell et al. 2004, Olszewski 2004, Crist and Veech 2006). Repeated measurements of diversity can be regarded as making up the highest intermediate level of diversity ( $\beta_m$ ).

TABLE 4. Three measures of  $\beta$ -diversity (Whittaker 1960, Wilson and Shmida 1984, Shmida and Wilson 1985, Magurran 1988).

Variables:

$\beta_W$  = Whittaker's measure

$\beta_C$  = Cody's measure

$\beta_T$  = Wilson and Shmida's measure

$S_{obs}$  = total species richness found in the system

$\bar{\alpha}$  = mean sample-level diversity, where diversity is measured as species-richness

G = number of species gained along a series of samples

L = number of species lost along a series of samples

Formulas:

Whittaker's measure:  $\beta_W = (S_{obs} / \bar{\alpha}) - 1$

Cody's measure:  $\beta_C = (G + L) / 2$

Wilson and Shmida's measure:  $\beta_T = (G + L) / 2 \bar{\alpha}$

As an alternate to the resampling method of partition estimation I also used rarefaction curves. The first point on the curve is mean richness at the first level:  $\alpha_1$  richness. Following the formula  $\gamma = \alpha_1 + \sum_{h=1}^m \beta_h$  (Table 5), the difference between the first and last points on the curve is the total  $\beta$ -richness for the system. Furthermore, in a second rarefaction curve that estimates accumulation of species by pimple instead of



transect, the first point on that curve would be the mean  $\alpha$ -level richness per pimple. The difference between the first point on the pimple-level curve and the first point on the transect-level curve equals  $\beta$ -level diversity among transects (Crist and Veech 2006). That is,  $\alpha_2 - \alpha_1 = \beta_1$ ; this relationship can be used with curves at each successive level to determine  $\alpha$ - and  $\beta$ -level richness (Gotelli 2001, Longino et al. 2002, Colwell et al. 2004, Olszewski 2004, Crist and Veech 2006).

## RESULTS

### *General descriptors*

*Pimple-level patterns.* The mean number of species found in each pimple across all years of the study was  $9.7 \pm 4$ , and annual mean species richness in pimples was significantly higher in 2006 than in either 2003 or 2004 (ANOVA;  $P < 0.01$ ; Fig. 5). There were significant differences in pimple-level diversity between pimples (ANOVA; richness:  $P < 0.001$ ; Shannon:  $P < 0.001$ ; Simpson's  $P < 0.02$ ; Fig. 6). Richness varied between pimples by a factor of three, and Shannon and Simpson's diversity indices also varied by an appreciable margin (FIG. 6). Variance in diversity does not appear to be determined by pimple size or location (FIG. 6), and I verified that observation with regression analysis (Fig. 7).

I performed regression analyses on the response of species richness to 1) different estimates of pimple size (e.g. maximum width east to west or north to south or maximum radius; Fig. 7A); as well as 2) different measures of pimple location (i.e. x or y coordinate on a map grid; Fig. 7B). Regression results did not indicate any significant relationships;  $R^2$  values were  $< 0.10$  and coefficients were  $< 0.001$ . Similarly, there was no relationship between either Shannon or Simpson's diversity indices and pimple size and position.

TABLE 5. Terms and formulas used in additive diversity partitioning (Crist et al. 2003, Olszewski 2004, Crist and Veech 2006).

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Variables:

- $\gamma$  = total species richness or diversity in study area;  $\gamma < \alpha_m$   
 $\alpha_h$  = average richness or diversity within sample units at level  $h$   
 $m$  = the highest level of study  
 $h = 1, 2, 3, \dots, m$  are all the levels of study  
 $\beta_h$  = average richness between sample units at level  $h$   
 $r_h$  = the number of sample units at level  $h$   
 $j$  = the sample number at a particular level, i.e.,  $j = 1, 2, 3, \dots, r_h$   
 $b_{hj}$  = the  $j$ th sample at level  $h$   
 $D_{hj}$  = the diversity metric recorded for the  $j$ th sample at level  $h$   
 $q_{hj}$  = the proportion of the number of individuals in sample  $j$  to the total number of individuals in all samples at level  $h$

Formulas:

total (landscape) diversity  $\gamma = \alpha_1 + \sum_{h=1}^m \beta_h$

average diversity at level  $h$ ; unequal sample weights:

$$\alpha_h = \sum_{j=1}^{r_h} D_{hj} q_{hj}$$

average diversity at level  $h$ ; equal sample weights (used in estimating partitions from rarefaction curves):

$$\alpha_h = \frac{1}{r_h} \sum_{j=1}^{r_h} D_{hj}$$

general equations for diversity among samples or higher levels ( $\beta$ -diversity)

$$1) \quad \beta_m = \gamma - \alpha_m$$

$$2) \quad \beta_h = \alpha_{h+1} - \alpha_h ; \text{ for } h < m$$

average diversity among samples at level  $h$  when  $D$  is measured as species richness; unequal sample weights

$$\beta_h = \sum_{j=1}^{r_h} q_{hj} (\gamma - D_{hj})$$

average diversity among samples at level  $h$  when  $D$  is measured as species richness; equal sample weights

$$\beta_h = \frac{1}{r_h} \sum_{j=1}^{r_h} (\gamma - D_{hj})$$


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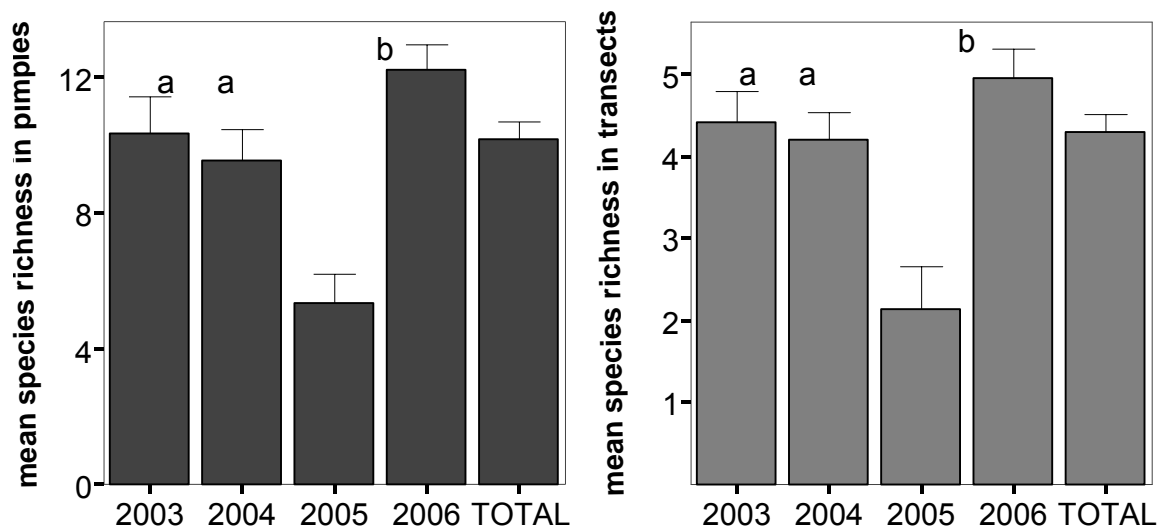


FIG. 5. Per-pimple and per-transect mean species richness by year with grand total mean. In this and subsequent figures, error bars represent one standard error of the mean and lowercase letters represent significantly homogeneous groupings (at  $p < 0.05$ ) based on Tukey's multiple comparisons test. The incomplete dataset from 2005 was not included in multiple comparisons.

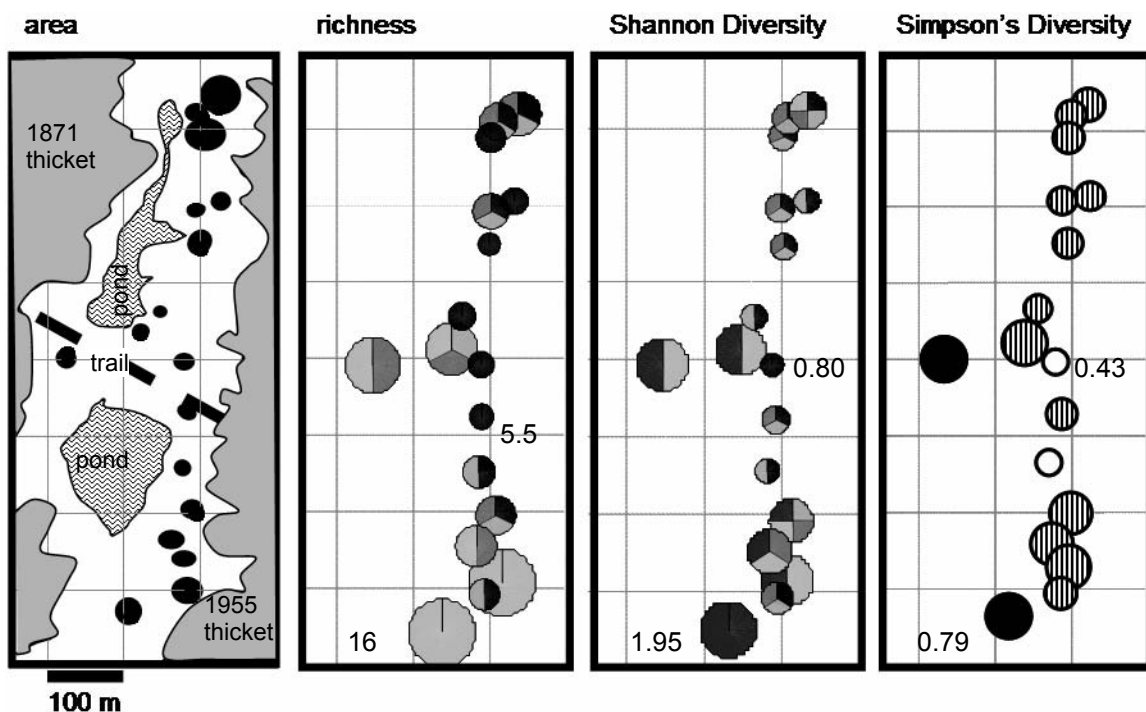


FIG. 6. Maps showing pimple sizes, richness, Shannon diversity, and Simpson's diversity. In the area map, dot size reflects area. In the diversity maps, relative positions of pimples are preserved, but the diameters of symbols indicate the relative values of each diversity metric. Numbers indicate maxima and minima for estimation of scale. Color patterns represent overlapping homogeneous subsets as determined with Tukey's test.

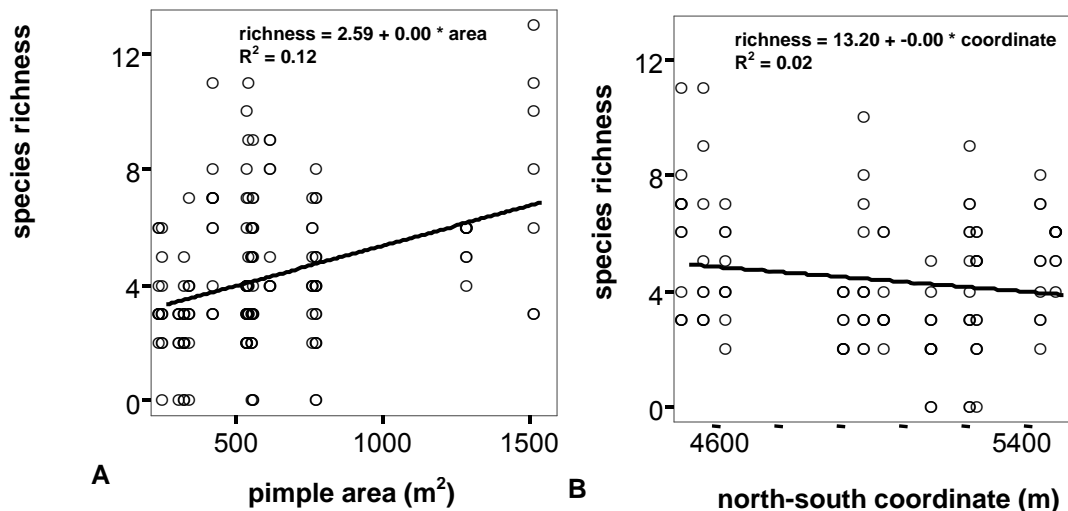


FIG. 7. Relationships of pimple size and location to richness.

*Transect-level patterns.* Mean richness per transect was  $4.3 \pm 2.5$  (Fig. 5). There was a significant effect of habitat type on species richness, Shannon diversity, and Simpson's diversity index; marsh and summit transects had higher mean values than shrub transects (ANOVA;  $P < 0.001$  for all three measures; Tukey's significant at  $P < 0.05$ ; Fig. 8, Fig. 9, & Fig. 10). Year of measurement had a significant effect on variation for each of the three metrics (ANOVA;  $P < 0.001$  for all three measures; Tukey's significant at  $P < 0.05$ ), but only the incomplete 2005 dataset was significantly different from other years. Analysis with 2005 data excluded revealed that there was no significant difference in species richness between 2003, 2004, and 2006, but there was a significant year effect with Shannon and Simpson's diversity with 2004 transects exhibiting higher diversity than the other two years (ANOVA;  $P < 0.05$  for both metrics; Tukey's significant at  $P < 0.05$ ).

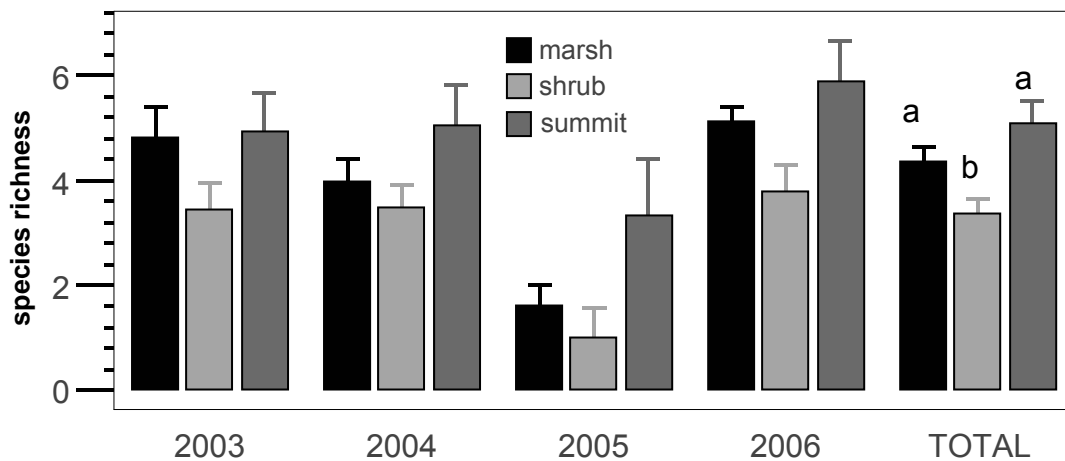


FIG. 8. Yearly mean transect-level species richness in each habitat type.

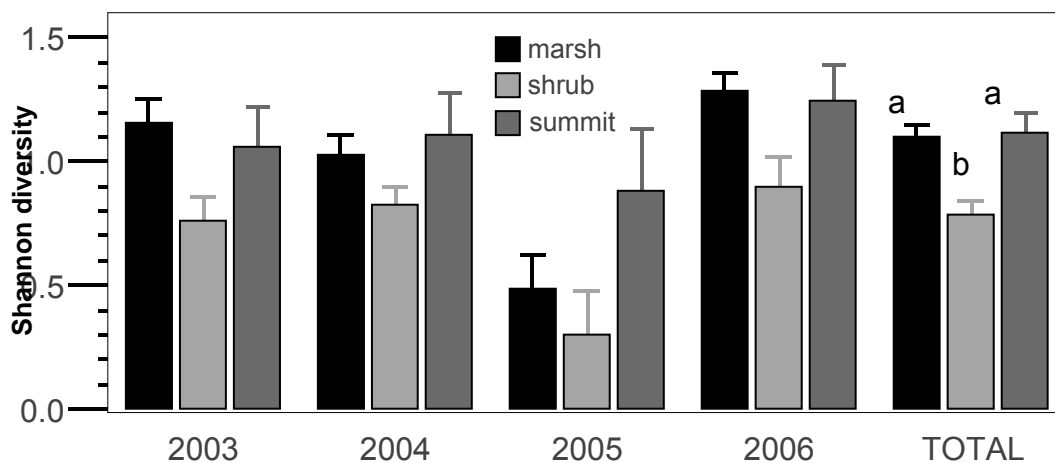


FIG. 9. Yearly mean transect-level Shannon diversity in each habitat type.

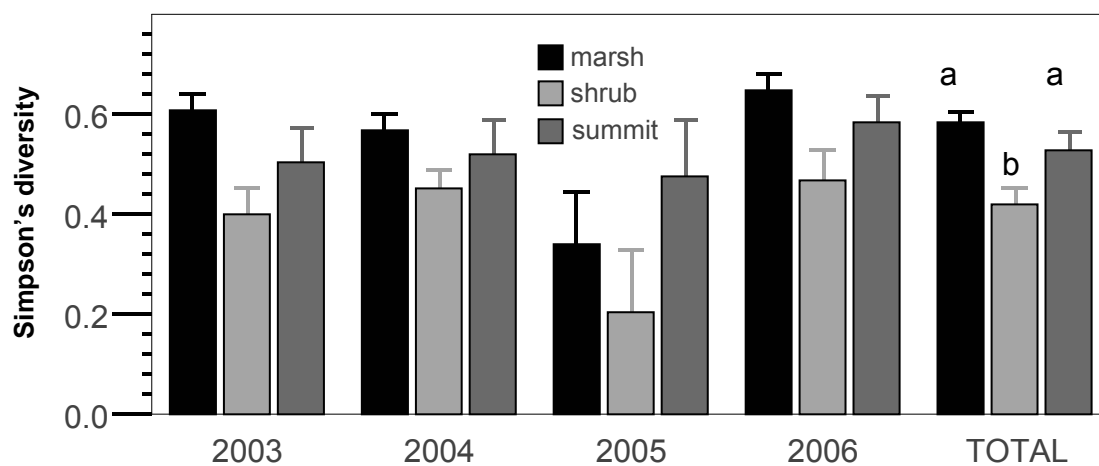


FIG. 10. Yearly mean transect-level Simpson's diversity index in each habitat type .

*Comparison to main dunes.* Mean richness on the main dunes was  $19.5 \pm 7.5$  per dune,  $6.8 \pm 2.5$  per  $25 \text{ m}^2$  plot, and  $3.8 \pm 1.6$  per  $.25 \text{ m}^2$  subplot. The richness of pimple summit transects at  $5.1 \pm 3.1$  falls between the plot and subplot richness of the main dunes (Fig. 11: B & C). Dune ridge reference plots did not have significantly different Shannon diversity than summit plots on pimples ( $1.05$  vs.  $0.98$ ;  $p = 0.2$ ), but did have significantly lower species richness ( $3.8$  vs.  $5$ ;  $p < 0.0001$ ).

*Importance values.* There were more infrequently-occurring species in pimple plots than commonly-occurring ones (Fig. 12; Table 6). The most commonly-occurring species was wax myrtle, *Morella cerifera*, which was also the most dominant (i.e., it represented the most coverage.) The ten most dominant and frequently-occurring species were all typical of shrub thicket or marsh. *Spartina patens*, a C4 grass, is commonly and generally found in both hydric and xeric habitats on Hog Island, but is infrequent on pimple summits. A few species were not found often but were very abundant when they occurred, e.g. duckweed, *Lemna minor*.

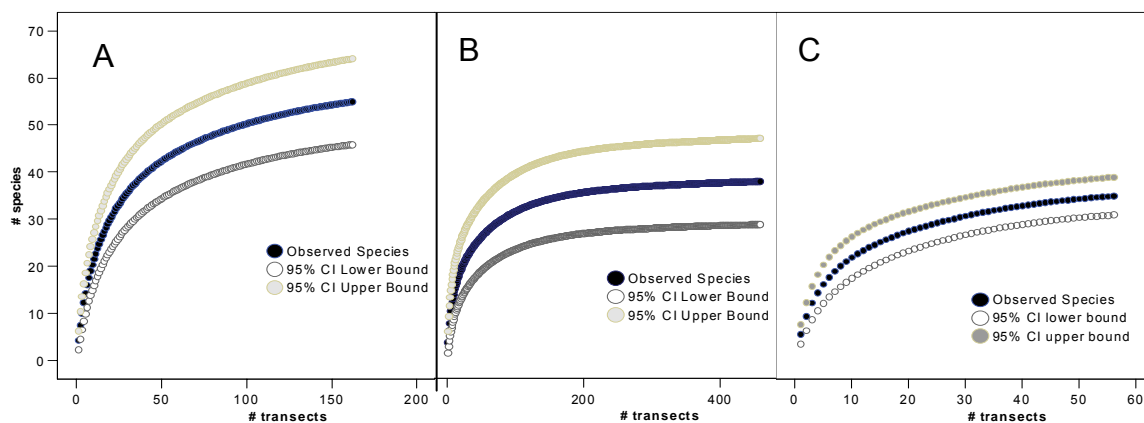


FIG. 11. Rarefaction curves of species encountered based on number of transects sampled. The curves are the product of an analytical procedure (Colwell et al. 2004) and are therefore not empirically-derived species–area curves. (A) Entire pimple richness. (B) Dune reference plots. (C) Pimple summits.

TABLE 6. Relative dominance and relative frequency for pimple species.  
 “ $IV_{mod}$ ” is a modified importance value: relative frequency plus relative dominance.

	Species	$IV_{mod}$	rank	Rel. Freq.	rank	Rel. Dom.
1	<i>Morella cerifera</i>	75.10%	1	20.03%	1	55.07%
2	<i>Polygonum hydropiperoides</i>	16.00%	3	8.12%	2	7.87%
3	<i>Parthenocissus quinquefolia</i>	12.51%	2	8.96%	6	3.55%
4	<i>Spartina patens</i>	11.66%	4	6.16%	3	5.50%
5	<i>Distichlis spicata</i>	9.67%	6	4.62%	4	5.05%
6	<i>Scirpus pungens</i>	6.62%	9	2.94%	5	3.68%
7	<i>Rubus argutus</i>	6.48%	8	3.92%	7	2.55%
8	<i>Carex albolutescens</i>	6.27%	5	5.04%	10	1.23%
9	<i>Mikania scandens</i>	5.28%	7	4.06%	11	1.22%
10	<i>Festuca rubra</i>	5.02%	10	2.80%	8	2.22%
11	<i>Rumex acetosella</i>	4.05%	11	2.66%	9	1.39%
12	<i>Juncus dichotomus</i>	3.52%	12	2.38%	12	1.14%
13	<i>Schizachyrium scoparium</i>	2.86%	14	1.82%	14	1.04%
14	<i>Baccharis halimifolia</i>	2.81%	16	1.68%	13	1.13%
15	<i>Cirsium horridulum</i>	2.78%	13	2.10%	18	0.67%
16	<i>Hydrocotyle verticellata</i>	2.36%	19	1.54%	16	0.82%
17	<i>Phragmites australis</i>	1.98%	18	1.54%	20	0.44%
18	<i>Cyperus strigosus</i>	1.96%	22	1.26%	17	0.70%
19	<i>Eupatorium hyssopifolium</i>	1.85%	21	1.26%	19	0.59%
20	<i>Prunus serotina</i>	1.78%	15	1.68%	31	0.10%
21	<i>Phyla lanceolata</i>	1.74%	17	1.54%	27	0.20%
22	<i>Panicum sp.</i>	1.53%	20	1.40%	28	0.13%
23	<i>Ammophila breviligulata</i>	1.46%	24	1.12%	22	0.34%
24	<i>Andropogon virginicus</i>	1.38%	25	0.98%	21	0.40%
25	<i>Persea palustris</i>	1.22%	23	1.12%	32	0.10%
26	<i>Lemna minor</i>	1.19%	42	0.28%	15	0.91%
27	<i>Juniperus virginianus</i>	0.96%	28	0.70%	25	0.26%
28	<i>Toxicodendron radicans</i>	0.90%	27	0.84%	39	0.06%
29	<i>Panicum lanuginosum</i>	0.88%	26	0.84%	41	0.04%
30	<i>Eupatorium capillifolium</i>	0.70%	36	0.42%	23	0.28%
31	<i>Teucrium canadense</i>	0.63%	31	0.56%	35	0.07%
32	<i>Typha latifolia</i>	0.63%	30	0.56%	36	0.07%
33	<i>Galium sp.</i>	0.61%	29	0.56%	40	0.05%
34	<i>Setaria geniculata</i>	0.55%	41	0.28%	24	0.27%
35	<i>Typha angustifolia</i>	0.54%	35	0.42%	29	0.12%
36	<i>Panicum amarum</i>	0.50%	40	0.28%	26	0.22%
37	<i>Pluchea odorata</i>	0.50%	34	0.42%	33	0.08%
38	<i>Panicum leucothrix</i>	0.44%	33	0.42%	43	0.02%
39	<i>Hypericum hypericoides</i>	0.43%	32	0.42%	46	0.01%
40	<i>Iva frutescens</i>	0.38%	39	0.28%	30	0.10%
41	<i>Fimbristylis caroliniana</i>	0.29%	38	0.28%	45	0.01%
42	<i>Linaria canadensis</i>	0.29%	37	0.28%	47	0.01%
43	<i>Euthamia capillifolium</i>	0.22%	52	0.14%	34	0.08%
44	<i>Ptilimnium capillaceum</i>	0.21%	51	0.14%	37	0.07%
45	<i>Panicum virgatum</i>	0.21%	50	0.14%	38	0.07%
46	<i>Samolus valerandi</i>	0.16%	49	0.14%	42	0.02%
47	<i>Hypochaeris radicata</i>	0.16%	48	0.14%	44	0.02%
48	<i>Boehmeria cylindrica</i>	0.15%	46	0.14%	49	0.01%
49	<i>Vitis sp.</i>	0.15%	47	0.14%	48	0.01%
50	<i>Panicum dichotomiflorum</i>	0.14%	45	0.14%	50	0.01%
51	<i>Kosteletskya virginica</i>	0.14%	44	0.14%	51	0.01%
52	<i>Juncus biflorus</i>	0.14%	43	0.14%	52	0.01%

In main dune plots, relative dominance and frequencies of species were notably different than in pimples, even when comparing the dune species only to transects from pimple summits (Table 7). Although there were 38 species found in both the reference and pimple summit plots, only 20 were shared between the two areas. The two most important species in the reference plots were dune-stabilizing grasses, and wax myrtle was only twentieth in importance rather than first, as in the pimple plots. In summit plots on pimples, shrub and marsh species were common (e.g. *Polygonum hydropiperoides*, *Parthenocissus quinquefolia*, and *Rubus argutus*), but infrequent or absent in dune plots.

#### *Rarefaction curves*

There were 52 species found in pimples during all four years of the study (Fig. 11A). The ICE and Chao 2 estimates of species richness were respectively 59.9 and 58.4 (Fig. 13). There were  $38 \pm 9.2$  (95% CI) species found in the main dunes, compared with  $35 \pm 4$  in the summit plots on pimples (Fig. 11 B&C).

#### *Ordinations*

Three different ordination techniques produced results that further established the difference between pimple plant assemblages and species composition in reference plots especially when comparing xeric transects, i.e., main dune and pimple summits. In both a Bray-Curtis ordination (Fig. 14) and a non-metric multidimensional scaling procedure (Fig. 15) describing relationships between transects, a few species were recurrently highly correlated to explanatory axes (Table 8). Those species included wax myrtle, (*Morella cerifera*); beach grasses (*Ammophila breviligulata* and *Panicum amarum*); xerophytic forbs (*Solanum carolinianum*, *Cirsium horridulum*, and *Rumex acetosella*);



hydrophytes (*Polygonum hydropiperoides* and *Carex albolutescens*); and woody species (*Prunus serotina* and *Parthenocissus quinquefolia*).

TABLE 7. Comparison of species importance value (modified), frequency, and dominance scores for species found in the main dunes of Hog Island and the summits of pimples. Species are listed in decreasing order of importance on the main dunes. Only importance value rankings are given; the modified importance value is the sum of relative frequency and relative dominance.

Species	Main Dunes					Pimple Summits				
	IV <sub>mod</sub> rank	relative frequency		relative dominance		IV <sub>mod</sub> rank	relative frequency		relative dominance	
<i>Ammophila breviligulata</i>	1	1	0.194	1	0.340	13	12	0.028	13	0.011
<i>Panicum amarum</i>	2	2	0.172	2	0.170	20	24	0.007	16	0.007
<i>Spartina patens</i>	3	3	0.109	3	0.093	4	7	0.045	3	0.062
<i>Rumex acetosella</i>	4	4	0.088	6	0.046	3	4	0.066	4	0.044
<i>Schizachyrium scoparium</i>	5	8	0.037	4	0.061	8	9	0.045	7	0.033
<i>Cirsium horridulum</i>	6	5	0.060	7	0.033	9	5	0.052	9	0.021
<i>Rubus argutus</i>	7	11	0.028	5	0.048	2	3	0.069	2	0.079
<i>Panicum sphaerocarpon</i>	8	9	0.037	8	0.031	-	-	-	-	-
<i>Eupatorium hyssopifolium</i>	9	6	0.040	10	0.022	11	11	0.031	11	0.019
<i>Prunus serotina</i>	10	7	0.040	9	0.022	17	17	0.024	24	0.002
<i>Solanum carolinianum</i>	11	10	0.037	13	0.015	-	-	-	-	-
<i>Eupatorium capillifolium</i>	12	14	0.016	11	0.021	19	19	0.010	14	0.009
<i>Juncus dichotomus</i>	13	13	0.020	12	0.016	7	6	0.049	6	0.035
<i>Aristida tuberculosa</i>	14	12	0.021	16	0.009	-	-	-	-	-
<i>Festuca rubra</i>	15	15	0.013	15	0.011	6	8	0.045	5	0.041
<i>Aralia spinosa</i>	16	16	0.010	14	0.013	-	-	-	-	-
<i>Panicum lanuginosum</i>	17	17	0.009	21	0.004	23	22	0.010	27	0.001
<i>Mikania scandens</i>	18	19	0.006	18	0.005	16	14	0.028	19	0.004
<i>Morella cerifera</i>	19	26	0.004	17	0.007	1	1	0.174	1	0.536
<i>Baccharis halimifolia</i>	20	18	0.006	20	0.005	30	30	0.003	21	0.003
<i>Apocynum cannabinum</i>	21	27	0.004	19	0.005	-	-	-	-	-
<i>Linaria canadensis</i>	22	20	0.005	25	0.002	27	27	0.007	33	0.000
<i>Centella erecta</i>	23	21	0.005	24	0.002	-	-	-	-	-
<i>Cyperus</i> sp.	24	22	0.005	26	0.002	-	-	-	-	-
<i>Gnaphalium chileensis</i>	25	30	0.003	22	0.003	-	-	-	-	-
<i>Strophostyles helvola</i>	26	23	0.005	27	0.002	-	-	-	-	-
<i>Linum medium</i>	27	28	0.004	23	0.002	-	-	-	-	-
<i>Gnaphalium purpurea</i>	28	25	0.004	28	0.002	-	-	-	-	-
<i>Fimbristylis caroliniana</i>	29	24	0.004	30	0.001	35	35	0.003	32	0.000
<i>Parthenocissus quinquefolia</i>	30	29	0.004	29	0.001	5	2	0.087	10	0.020
<i>Linum virginianum</i>	31	31	0.003	32	0.001	-	-	-	-	-
<i>Monarda punctata</i>	32	33	0.002	31	0.001	-	-	-	-	-
<i>Conzya (Erigeron)</i> <i>canadensis</i>	33	32	0.002	34	0.001	-	-	-	-	-
<i>Hypericum hypericoides</i>	34	35	0.002	33	0.001	29	29	0.007	38	0.000
<i>Elymus virginianus</i>	35	34	0.002	35	0.001	-	-	-	-	-

(Table 7, continued)

Species	$IV_{mod}$ rank	relative frequency	relative dominance	$IV_{mod}$ rank	relative frequency	relative dominance
<i>Euphorbium ammonoides</i>	36	36	0.001	36	0.000	- - - - -
<i>Juncus canadensis</i>	37	37	0.001	37	0.000	- - - - -
<i>Lepidium virginianum</i>	38	38	0.001	38	0.000	- - - - -
<i>Polygonum</i>						
<i>hydropiperoides</i>	-	-	-	-	10	15 0.024 8 0.028
<i>Carex albolutescens</i>	-	-	-	-	12	10 0.038 17 0.006
<i>Andropogon virginicus</i>	-	-	-	-	14	16 0.024 12 0.013
<i>Panicum sp.</i>	-	-	-	-	15	13 0.028 18 0.004
<i>Juniperus virginianus</i>	-	-	-	-	18	18 0.017 15 0.008
<i>Phragmites australis</i>	-	-	-	-	21	20 0.010 20 0.003
<i>Toxicodendron radicans</i>	-	-	-	-	22	21 0.010 25 0.001
<i>Persea palustris</i>	-	-	-	-	24	23 0.010 28 0.001
<i>Scirpus pungens</i>	-	-	-	-	25	25 0.007 26 0.001
<i>Panicum leucothrix</i>	-	-	-	-	26	26 0.007 30 0.000
<i>Hydrocotyle verticellata</i>	-	-	-	-	28	28 0.007 34 0.000
<i>Euthamia capillifolium</i>	-	-	-	-	31	31 0.003 22 0.002
<i>Panicum virgatum</i>	-	-	-	-	32	32 0.003 23 0.002
<i>Hypochaeris radicata</i>	-	-	-	-	33	33 0.003 29 0.001
<i>Teucrium canadense</i>	-	-	-	-	34	34 0.003 31 0.000
<i>Boehmeria cylindrica</i>	-	-	-	-	36	36 0.003 35 0.000
<i>Vitis sp.</i>	-	-	-	-	37	37 0.003 36 0.000
<i>Panicum dichotomiflorum</i>	-	-	-	-	38	38 0.003 37 0.000

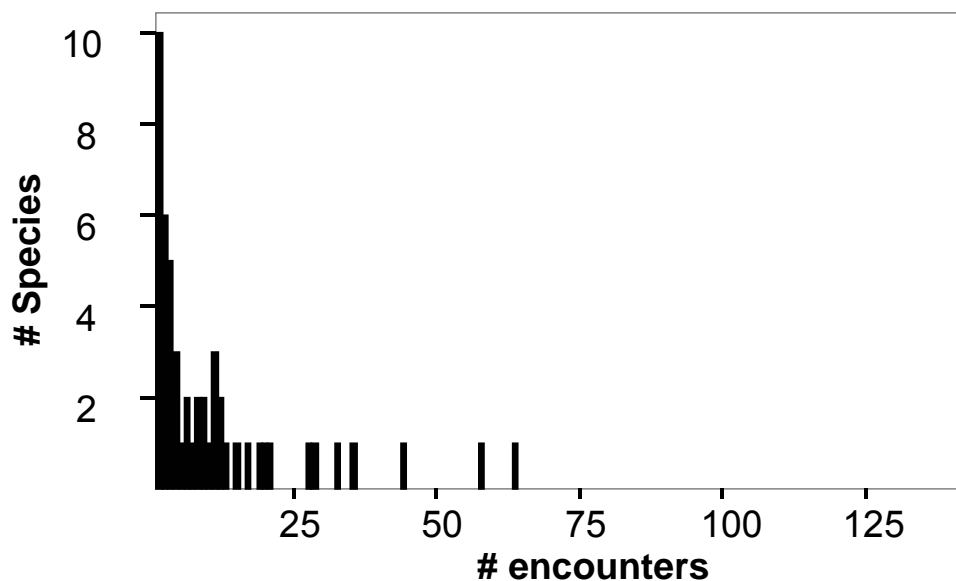


Fig. 12. Histogram of pimple species frequency.

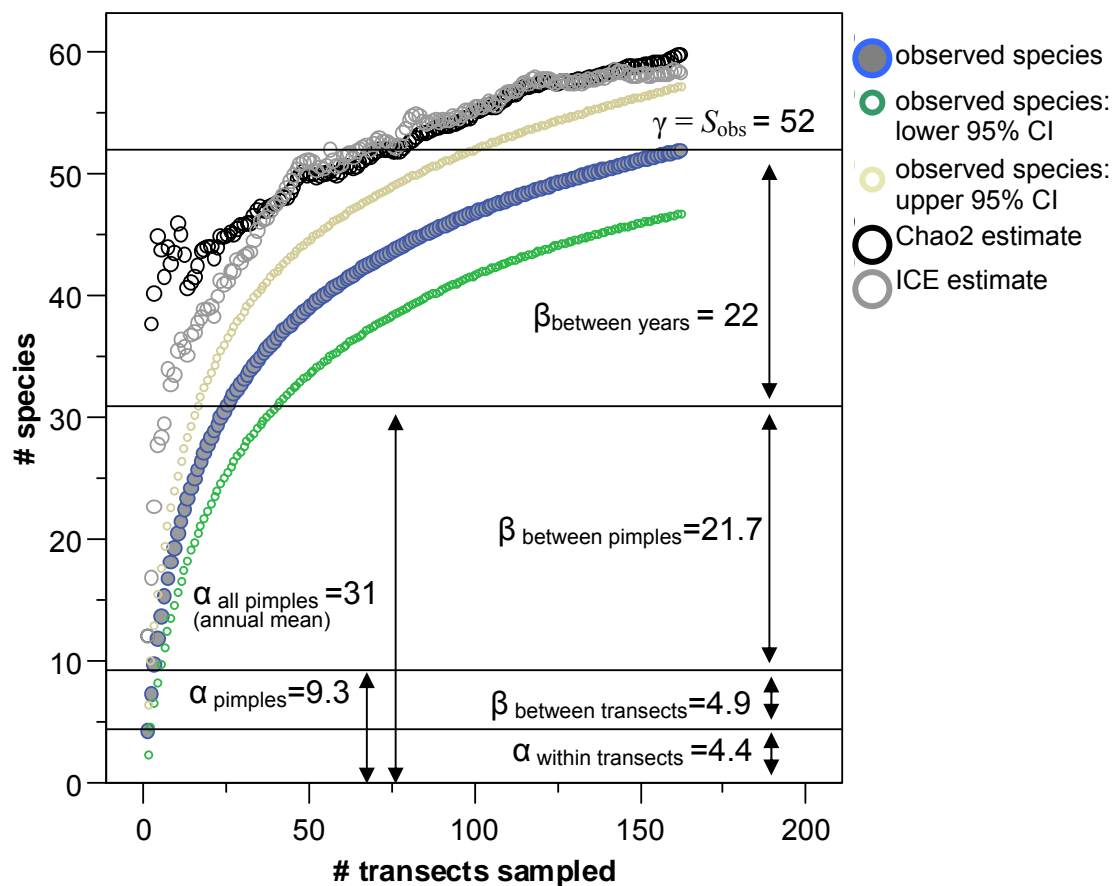


FIG. 13. Rarefaction curve showing partitions of diversity, observed species richness ( $S_{\text{obs}}$ ) with confidence intervals, and two richness estimators: ICE and Chao 2.

Principal components analysis performed worse than the other two ordination methods in explaining variation and resolving relationships, based on percent variation explained by each axis (Fig. 16). Transects were crowded in the PCA ordination space, apparently because of a few dune reference plots and the data from five Parramore Island pimples. Removing these transects did not appreciably improve the data resolution. In all ordinations, groupings of transects especially dune plots and pimple summits are distinct.

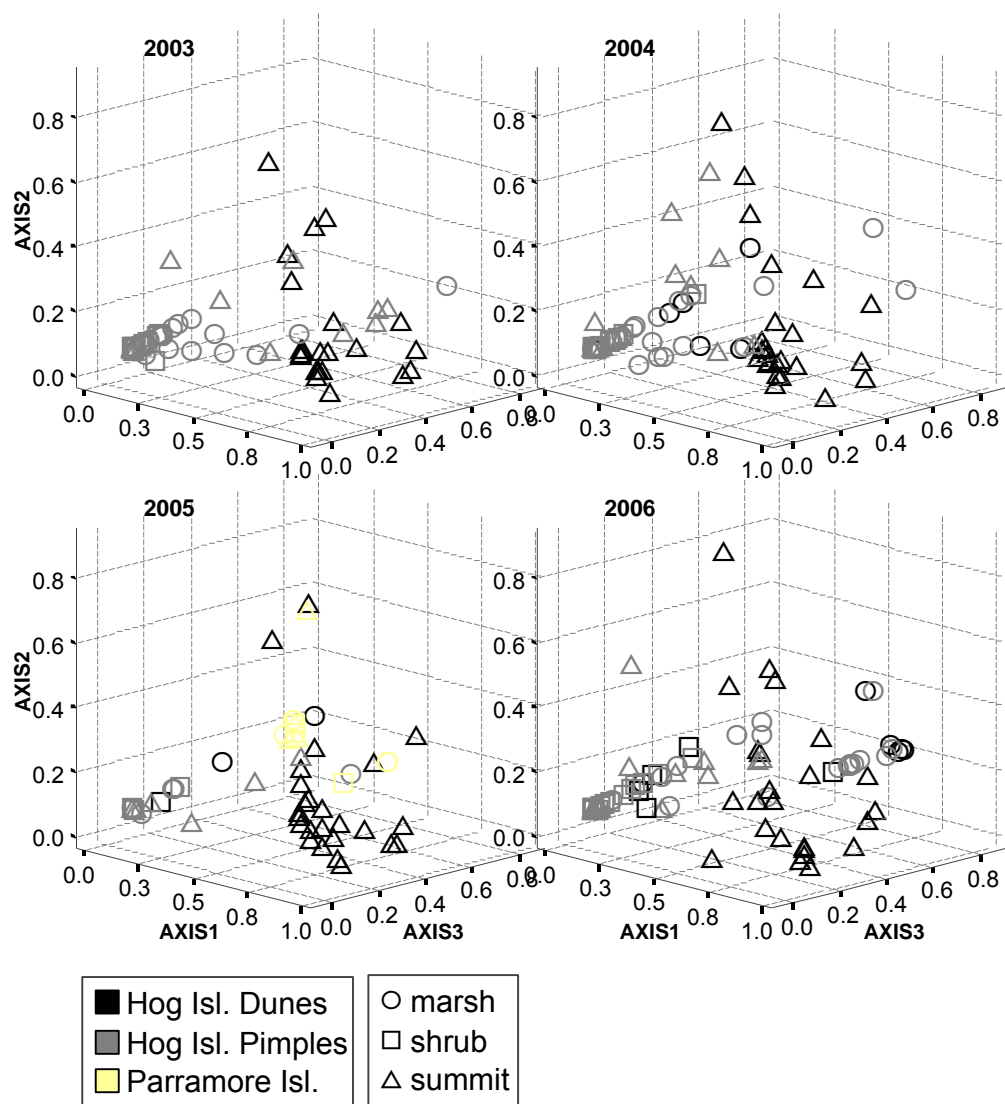


FIG. 14. Three axes of a Bray-Curtis ordination of transects based on species abundances. Axes 1-3 explain 37%, 7%, and 11% of variation in the data, respectively. Ordination was performed on data from all years combined; the plot was divided by year to increase clarity.

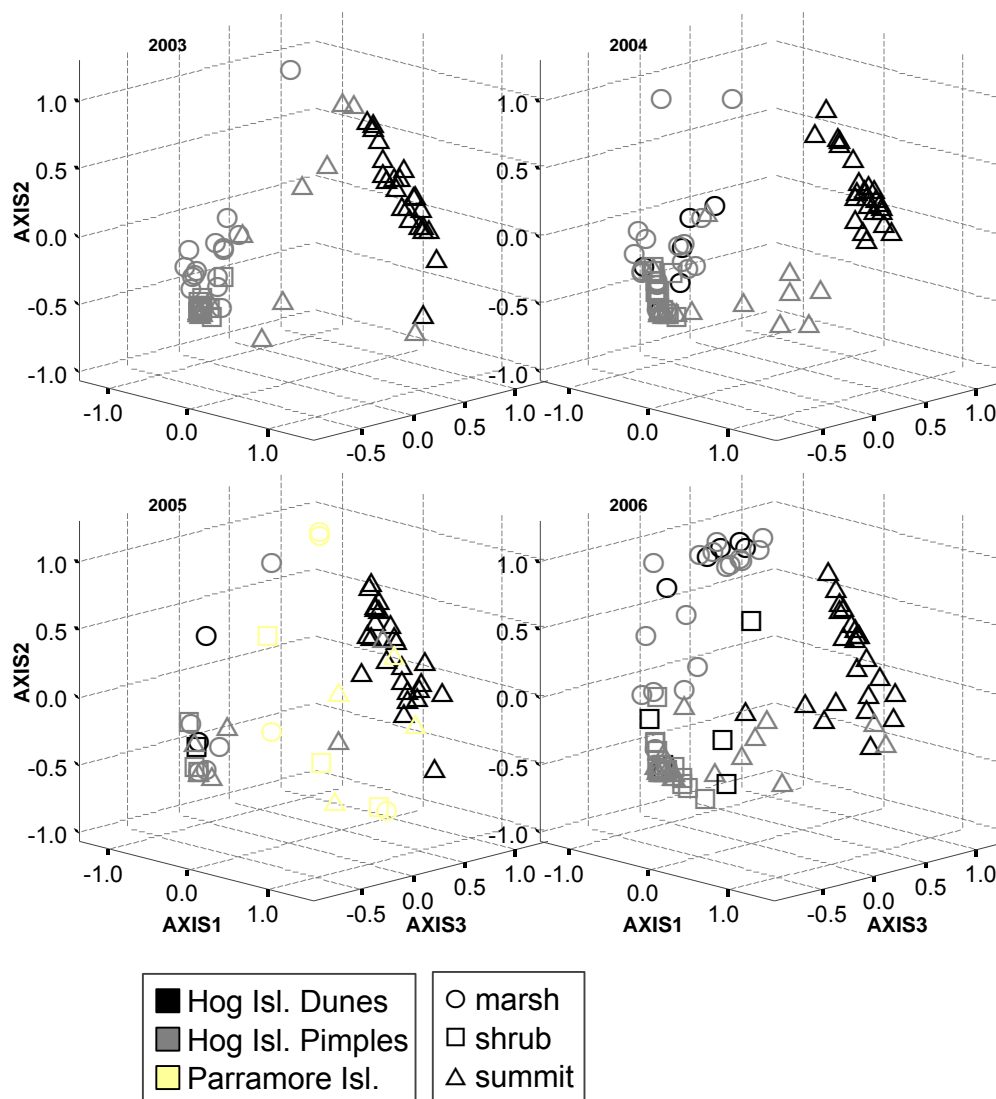


FIG. 15. Non-metric multidimensional scaling of transects based on species abundances. An autopilot procedure determined that a three-axis ordination would provide the maximum amount of explanatory power. Axis 1 explains 25% of variation; Axis 2 21%; and Axis 3 36%. Ordination was performed on data from all years combined; the plot was divided by year to increase clarity.

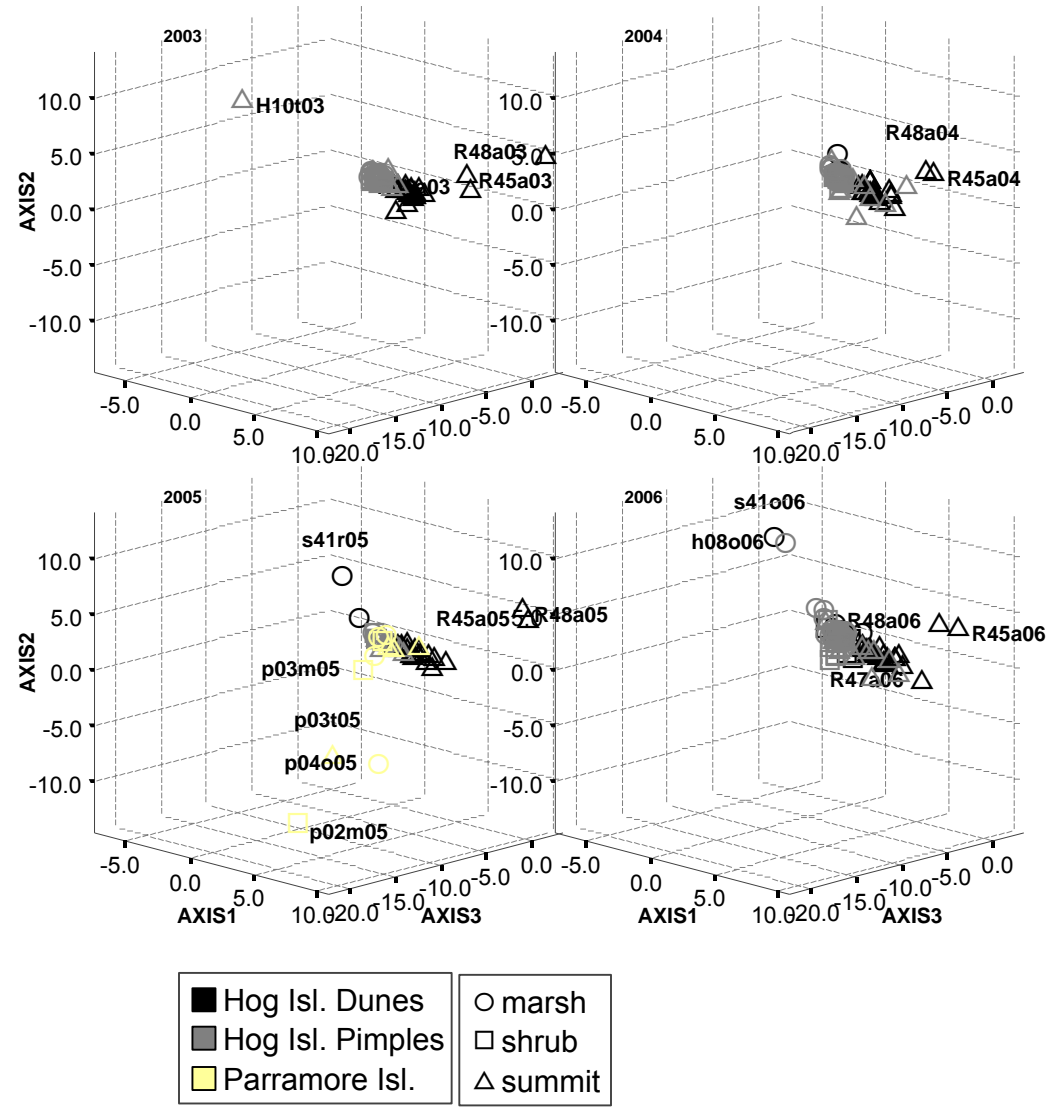


FIG. 16. Principal components analysis for transects based on species abundances. Axes 1-3 explained 5%, 4%, and 4%, respectively. Ordination was performed on data from all years combined; the plot was divided by year to increase clarity.

TABLE 8. Explanatory value of first three axes of Bray-Curtis ordination and non-metric multidimensional scaling and the ten most important species in each based on correlation (Pearson's r).

Bray-Curtis Ordination		Non-Metric Multidimensional Scaling	
Axis 1		Axis 1	
37%	r	25%	r
<i>Morella cerifera</i>	0.832	<i>Morella cerifera</i>	0.481
<i>Ammophila breviligulata</i>	0.459	<i>Spartina patens</i>	0.433
<i>Panicum amarum</i>	0.386	<i>Scirpus pungens</i>	0.136
<i>Solanum carolinianum</i>	0.093	<i>Panicum amarum</i>	0.061
<i>Spartina patens</i>	0.076	<i>Festuca rubra</i>	0.047
<i>Cirsium horridulum</i>	0.068	<i>Parthenocissus quinquefolia</i>	0.037
<i>Rumex acetosella</i>	0.066	<i>Dichanthelium sphaerocarpon</i>	0.027
<i>Carex albolutescens</i>	0.053	<i>Carex albolutescens</i>	0.024
<i>Prunus serotina</i>	0.053	<i>Fimbristylis caroliniana</i>	0.023
<i>Polygonum hydropiperoides</i>	0.036	<i>Solanum carolinianum</i>	0.023
Axis 2		Axis 2	
7%	r	21%	r
<i>Schizachyrium scoparium</i>	0.832	<i>Morella cerifera</i>	0.681
<i>Morella cerifera</i>	0.459	<i>Ammophila breviligulata</i>	0.581
<i>Aristida tuberculosa</i>	0.386	<i>Panicum amarum</i>	0.412
<i>Euphorbia ammonoides</i>	0.093	<i>Solanum carolinianum</i>	0.096
<i>Cyperus</i> sp.	0.076	<i>Polygonum hydropiperoides</i>	0.087
<i>Dichanthelium sphaerocarpon</i>	0.068	<i>Cirsium horridulum</i>	0.083
<i>Rumex acetosella</i>	0.066	<i>Rumex acetosella</i>	0.068
<i>Linaria canadensis</i>	0.053	<i>Prunus serotina</i>	0.067
<i>Eupatorium hyssopifolium</i>	0.053	<i>Carex albolutescens</i>	0.055
<i>Juncus dichotomus</i>	0.036	<i>Parthenocissus quinquefolia</i>	0.047
Axis 3		Axis 3	
11%	r	11%	r
<i>Scirpus pungens</i>	0.832	<i>Baccharis halimifolia</i>	0.230
<i>Spartina patens</i>	0.459	<i>Phyla lanceolata</i>	0.179
<i>Ammophila breviligulata</i>	0.386	<i>Scirpus pungens</i>	0.155
<i>Morella cerifera</i>	0.093	<i>Juniperus virginiana</i>	0.112
<i>Panicum amarum</i>	0.076	<i>Mikania scandens</i>	0.101
<i>Galium</i> sp.	0.068	<i>Galium</i> sp.	0.076
<i>Phyla lanceolata</i>	0.066	<i>Festuca rubra</i>	0.065
<i>Phragmites australis</i>	0.053	<i>Teucrium canadense</i>	0.059
<i>Boehmeria cylindrica</i>	0.053	<i>Eupatorium capillifolium</i>	0.058
<i>Dichanthelium</i> sp.	0.036	<i>Boehmeria cylindrica</i>	0.055

### Diversity partitioning

Between-transect beta diversity as measured by three different indices was significantly higher in 2006 than in other years measured (Fig. 17). When comparing beta diversity among pimples, the three measures produced markedly different results in some instances (e.g., compare the pimple marked with a \* in Fig. 18). Conversely, some pimples had consistently high or low beta-diversity levels (e.g., the two marked with \*\* and \*\*\* in Fig. 18).

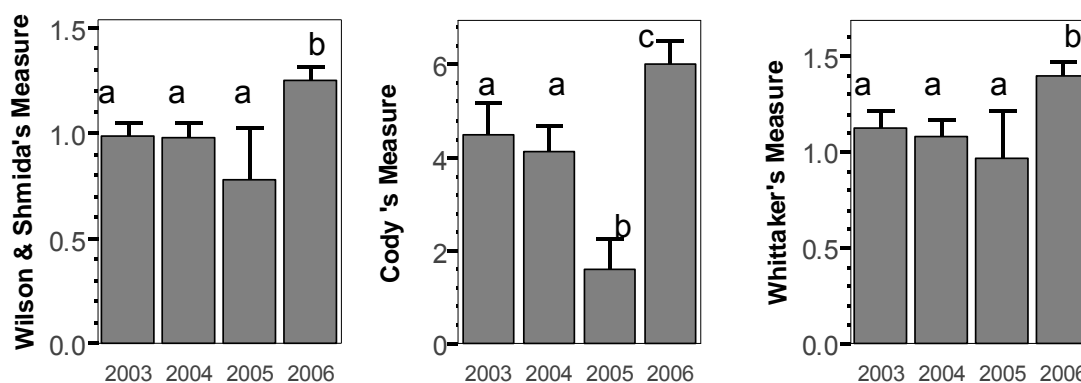


FIG. 17. Comparison of three measures of beta diversity between transects in pimples by year (Magurran 1988).

Analysis of spatial partitioning of diversity revealed different patterns for species richness, Simpson's diversity, and Shannon diversity (Fig. 19). Mean richness and diversity indices in transects were significantly lower than would be expected by random chance. The same pattern held for total annual mean richness and diversity. Partitions determined for dune reference plots nearly exhibited the opposite pattern, having more species per subplot than expected, and fewer per plot and dune line.



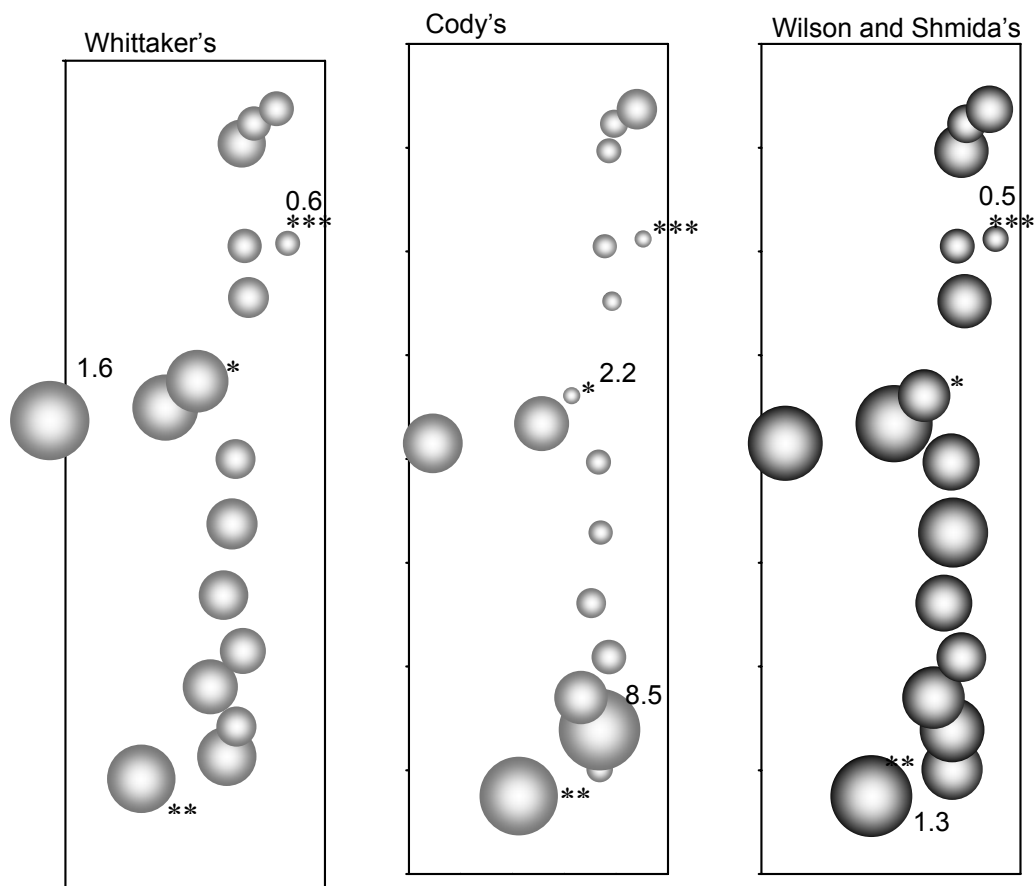


FIG. 18. Maps of three measures of beta diversity between transects in pimples. Asterisks are for emphasis; numbers indicate maxima and minima for each map.

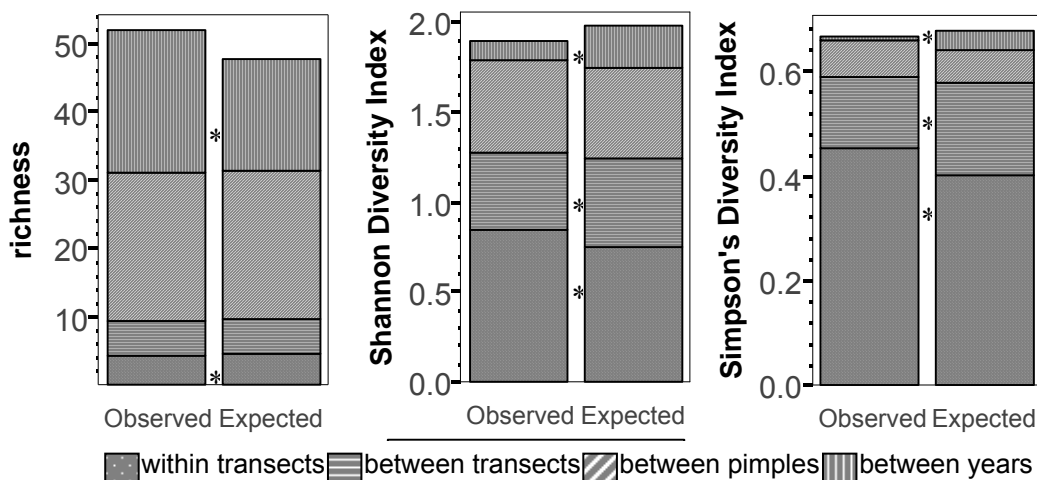


FIG. 19. Diversity partitioning within pimples as measured by three diversity indices. Expected partitions (i.e. null value estimates) are based on 10,000 resampling iterations performed with PARTITION (Crist and Veech 2006). \* Observed value was either > 95% of the estimated simulations or < 5% of simulated values.

TABLE 9. Diversity partitioning within and among pimples and within and among the main dunes as calculated with PARTITION.

\*P-value is the proportion of null values with a diversity estimate greater than the observed. Significant probabilities are in **boldface type**. \*\*Null-value estimates made from 10000 randomizations.

		Species Richness			Shannon Diversity			Simpson's Index		
		Obs.	Exp.**	P*	Obs.	Exp.**	P*	Obs.	Exp.**	P*
<b>Pimples</b>										
Total: (gamma)		52			1.979			0.678		
Years	alpha:	31	36	<b>1</b>	1.745	1.866	<b>0.998</b>	0.639	0.670	<b>0.986</b>
	beta:	21	17	<b>0</b>	0.233	0.112	<b>0.002</b>	0.039	0.008	<b>0.014</b>
Pimples	alpha:	9	9.4	0.545	1.247	1.23	0.152	0.579	0.5693	0.127
	beta:	22	21.6	0.217	0.498	0.515	0.832	0.060	0.0695	0.871
Transects	alpha:	4	4.7	<b>1</b>	0.754	0.848	<b>1</b>	0.403	0.453	<b>1</b>
	beta:	5	5	0.508	0.493	0.424	<b>0</b>	0.176	0.136	<b>0</b>
<b>Main dunes</b>										
Total: (gamma)		39			0.8143			2.215		
Years	alpha:	30.3	30.3	<b>0</b>	0.7982	0.7982	<b>0</b>	2.053	2.053	<b>0</b>
	beta:	8.7	8.7	<b>0</b>	0.0161	0.0161	<b>0</b>	0.162	0.162	<b>0</b>
Dune ridges	alpha:	17.1	19.8	<b>1</b>	0.7621	0.776	<b>0.9833</b>	1.806	1.899	<b>1</b>
	beta:	13.2	10.5	<b>0</b>	0.0361	0.0222	<b>0.016</b>	0.247	0.154	<b>0</b>
Plots	alpha:	6.6	9	<b>1</b>	0.614	0.7076	<b>1</b>	1.155	1.534	<b>1</b>
	beta:	10.5	8.1	<b>0</b>	0.1481	0.0545	<b>0</b>	0.651	0.272	<b>0</b>
Subplots	alpha:	3.7	3.4	<b>0</b>	0.5593	0.5443	<b>0</b>	0.89	0.812	<b>0</b>
	beta:	2.9	2.9	0.2335	0.0547	0.0758	<b>1</b>	0.265	0.295	<b>1</b>

## DISCUSSION

### *General descriptors*

*Pimple-level patterns.* Pimples were surprisingly species rich, considering their small size and the relatively harsh environment on the islands (Ehrenfeld 1990). The variability in diversity between pimples is also noteworthy. It should be considered as a

starting point for future study, and anyone using pimples as replicated study sites should consider their heterogeneity.

Lack of a relationship between pimple size and different measures of diversity was unexpected, since the species–area relationship is a basic tenet of ecology (Gleason 1925, MacArthur et al. 1966, Connor and McCoy 1979, Diamond 1988). Crist and Veech (2006), however, have found that the relationship between area (or sampling effort) and richness or diversity is often minimal. The close proximity of pimples to each other likely promotes propagule transfer and may diminish the relationship (MacArthur et al. 1966). That species richness (albeit not composition) is identical on pimple summits and dune ridges also suggests that species dispersal and colonization of the patchy habitats on the island is not overly influenced by patch size (Fahrig 1990, Burton and Bazzaz 1995, Planty Tabacchi et al. 1996, Tilman 1997, Aguiar and Sala 1999).

Lack of a relationship between geographic position and diversity also suggests that species distribution is fairly uniform across the northern end of Hog Island. When evaluating pimples as experimental units, lack of species–area and species–location relationships could be cited as a measure of uniformity among them. This finding does not, however, suggest that pimples are representative of habitat conditions on the island at large. There appears to be a bimodal distribution of species richness along the north–south gradient, since most of the less diverse pimples were in the center of the study area (Gauch and Chase 1974, Peet and Loucks 1977, Gauch and Stone 1979, ter Braak 1986, Allen et al. 1991, Peltzer et al. 1998). Perhaps there is a disturbance effect from proximity to the vehicle trail, but this is unlikely since vehicle use and even foot traffic is very limited on the island (Hosier and Eaton 1980).

*Transect-level patterns.* The significant effect of habitat type in explaining variation in richness and diversity indices is a good indicator that the zones are indeed distinct. The significant drop in richness in the shrub zone of pimples is largely due to competition from wax myrtle (Smith et al. 1995, Tolliver et al. 1995, Adler et al. 1998). The high diversity on pimple summits indicates that the dense shrub thickets are not a barrier to seed dispersal, even with species that are not typically wind or animal dispersed.

Of all the dominant species on pimples and the entire island, wax myrtle, *M. cerifera*, is by far the most important in terms of abundance (Young 1992, Young et al. 1995b). Most of the other important species are either marsh graminoids and forbs or other woody and sub-woody species. This suggests either that habitats are less heterogeneous in marsh and shrub zones relative to summit zones, i.e. fewer niches, or that there are fewer species suited to living in those zones, a historical artifact reflecting the suite of species that colonized the island (Diamond 1988, Houle 1997, Hofer et al. 2004).

### *Ordinations*

The dissimilarity of species relative dominance, relative frequency, and importance values between main dune plots and pimple summits is reflected in the groupings of transects in the ordinations performed on the species abundance data. Xeric plots are generally the most widely dispersed group of transects, relative to marsh and shrub plots, and within that cloud of points, pimple summit plots are segregated from dune plots, with the latter seeming to create a more uniform group (i.e. a tight group of nearly-overlapping points). Marsh plots also form distinct groups, but these groups have

the occasional intrusion of shrub transect within them and the distinction between reference plots and pimple plots is not as sharply defined. Shrub plots formed the tightest groupings, meaning that transects exhibited the least variation. Pimple and reference shrub plots overlapped frequently. The similarity of species composition in pimple and reference shrub zones is most likely a result of light competition from wax myrtle and subsequent reduction in species richness and abundance in the understory.

There were clear differences between pimple and dune plots, especially among the xeric samples. This evidence suggests that pimples are not exact replicates of island plant assemblages and may not be good models to use as experimental units. Most of the dune reference plots are in the center of dune summits and several meters away from the edge of the wax myrtle thickets, whereas most pimples have an open summit of only a few meters across, many with varying levels of canopy closure. Presence of wax myrtle and other shrub and shrub-edge species is likely a primary reason for assemblage structure differing between dunes and pimple summits. This suggests that xeric habitat conditions on main dunes may not be closely approximated by pimple summits.

Of the three ordination methods used, NMS and Bray-Curtis ordinations provided markedly greater explanation of variation over PCA. This suggests that species are responding to environmental factors in a nonmonotonic fashion (i.e., not linearly along one resource gradient) and indicates a high level of complexity of species abundances within pimple plant assemblages (Palmer 2007). The next chapter will explore the factors to which species are responding.

### *Rarefaction curves*

The ICE and Chao 2 estimates were greater than observed species richness suggesting that species richness may have been underestimated in floristic studies (Summerville and Crist 2002, Veech et al. 2002, Crist and Veech 2006). Low richness and diversity in shrub plots reflect the density of the thicket canopy. Although *M. cerifera* is a nitrogen-fixing species and deposits nitrogen-rich litter, it evidently grows too densely to allow many species to grow underneath it (Sande and Young. 1992, Young 1992, Smith et al. 1995, Tolliver et al. 1995, Adler et al. 1998, Crawford and Young 1998a, Wijnholds and Young 2000). High diversity and richness in summit plots suggests diverse environmental conditions or niches within those areas of pimples relative to other zones (Gauch 1982a, Palmer 2007). The rarefaction curve of dune reference plots seems to be closer to reaching an asymptote compared to the curve for pimple summits.

### *Diversity partitioning*

The higher beta diversity measured in 2006 is difficult to explain. I was the only person making field identifications, so there is little reason to believe that my personal accuracy or bias changed dramatically in the fourth year. The differences in the 2005 survey are readily explained by smaller data set and timing of the survey (i.e., beginning rather than height of the growing season). The 2005 season may also have been affected by the late summer.

Diversity partitioning helped to describe the assemblage structure on pimples and the main dunes. There was nearly equal  $\alpha$ - and  $\beta$ -richness within and between transects, which indicates that there was nearly complete turnover of species from one habitat zone to the next (Crist et al. 2003, Crist and Veech 2006). That, in turn, is an indication of

successful *a priori* stratification of transects on the pimples. Mean annual richness for all pimples was around three times greater than mean per-pimple richness, total richness over the entire four years of the study was even greater, and annual variations in richness and diversity were significantly different from random. This means that there was a definite variation in assemblage structure among pimples and that there was a shift in species composition over the years (Summerville and Crist 2005). Although some of this change can be attributed to measurement error and (in the case of annual variation) an artifact of the aberrant 2005 data set, it is still evidence of significant spatial and temporal variation in assemblage structure on pimples.

There are significantly non-random changes in diversity between plots within each of the three main dune lines and between the dune lines themselves. The latter finding can be explained by the differing ages of the dunes and presumably different successional stages existing in each. The former is explainable by the heterogeneity of placement of the plots within each ridge. There was no significant difference between observed annual changes and those expected at random. This implies that spatial variation in main dunes is similar to that in pimples but temporally, main dune assemblages are more stable (Summerville and Crist 2005).

## CONCLUSIONS

At the beginning of this study, the zonation of plant assemblages on pimples and the main dunes appeared similar. Although pimples apparently have similar species richness and diversity patterns as the dunes near them, the actual assemblage composition appears to differ. Pimples also seem to be more prone to shifts in species assemblage than

do the main dunes. Pimple summit communities are the most species-diverse and putatively most diverse relative to the other zones. Summits also have apparently more edge effect than the wider areas of dune xeric patches and more overlap in species composition with shrub and marsh assemblages. All of these factors should be seen as caveats if using pimples as experimental units. Species assemblages on pimples do not exactly duplicate those on main dunes.

These differences in species composition between pimples and main dunes are likely related to the ways in which each form. Whether biology drives geology during the formation of pimples or the reverse remains to be determined. In the case of tundra tree islands there apparently has to be a tree colonizing first before , although abiotic factors may influence establishment (Thomson 1950, Meredith 1972, Marr 1977, Davis 1980, Benedict 1984, Holtmeier and Broll 1992, Pauker and Seastedt 1996, Parker and Sanford 1999, Seastedt and Adams 2001). With tree islands in swamps, a geologic formation must be in place before the community can become established (Svihla 1930, 1939, Loveless 1959, Rich and Spackman 1979, Duever and Riopelle 1983, Troxler Gann et al. 2005). Future studies comparing pimples of different ages may resolve this question.

The newer or less commonly used mathematical methods employed for this study show promise for future fieldwork. When comparing statistical methods used in this study, ordinations have some definite advantages over general linear models (ANOVAs). There is no need for *a priori* construction of models, no concerns over loss of degrees of freedom, and more robust handling of data sets with many transects and species (Palmer, 2007). Moreover, the graphical representation of variations and associations between transects (or species) can make interpreting results more intuitive, albeit more artful.



Although it would be ideal to have a prior idea of the nature of variance in species responses and to choose an ordination technique accordingly, *a posteriori* comparison of ordination results provided valuable insight into the nature of variation in species responses, namely that species are responding in a nonmonotonic fashion to environmental gradients. Partition estimation of diversity has the decided advantage over the formulaic measures of calculating  $\beta$ -diversity, since it provides measures of diversity in the same units at all levels. The more standard measures of  $\beta$ -diversity only allowed for cross comparison within one level.

## CHAPTER 4

### ENVIRONMENTAL INFLUENCES ON SPECIES DISTRIBUTION

#### INTRODUCTION

A basic research goal of plant ecology is to understand the influences of environment on assemblage structure (Hayden et al. 1995). This is important and fundamental for understanding assemblage-level, community-level, and ecosystem-level functioning and has practical uses for ecosystem monitoring and restoration. The plant assemblages and ecosystems of barrier islands and dunes were among the first to be studied by ecologists, e.g., (Cowles 1899, Kearney 1904). Olsson-Seffer wrote in 1909 that “In discussing the factors that influence plant life [on dunes], I have found it convenient to classify them into the following groups: atmospheric, hydrodynamic, edaphic, topographic, and historical factors.” A century later, much remains to be understood about their ecology (Ehrenfeld 1990).

The readily apparent ecological driver on the islands is water. The position of the rain-charged fresh water table relative to the soil surface is the primary determinant of community type in the interior of barrier islands at the VCR. The difference between freshwater marsh, shrub or bramble thickets, and xeric dunes is apparently the result of distance above the fresh water table (Hayden et al. 1991, Hayden et al. 1995).

‘Elevational’ ranges containing those communities are narrow, on the scale of decimeters. Despite its apparent importance, availability of fresh water can only explain gross differences between communities and their inherent plant assemblages. In that case, species composition in assemblages should be largely uniform at equal elevations on each island. I have not observed that to be true.

There are a few approaches to describing and defining the role of environment in determining species composition. Experimental tactics would be to use reciprocal transplants, glass house experiments under different conditions, and experimental modification of assemblage composition, i.e., removal or addition of species (Tilman 1997). Alternatively, descriptive studies relating species abundances to environmental variables can be used in multivariate analyses and ordinations (Peet and Loucks 1977, Gauch 1982a, Pielou 1984, Peet et al. 1988, Palmer 2007).

I hypothesize that there are synergistic effects between water table, soil, landscape, and biota that elicit variation in plant species abundances within each community zone. This is not a novel idea in plant ecology (Olsson-Seffer 1909, Curtis and McIntosh 1951, Peet and Loucks 1977, Gauch 1982a, Pielou 1984, Peet et al. 1988, Frego and Carleton 1995, Bazzaz 1996, Palmer 2007), but there is nothing approaching a unified theory of plant species–environment interaction as yet. I studied relationships between plant assemblage composition and microhabitat conditions to determine what drivers were creating such tightly-packed habitat zones and to see if there were differences in species – environment interactions between pimples and main dunes.

#### MATERIALS AND METHODS

The study area and floristic survey methodology are the same as described in Chapters 2 and 3. Besides taking the plant censuses, I also collected environmental data and analyzed them as described below.

##### *Environmental measurements: hydrology*

To determine depth to water table at a transect, I used a 10 cm–diameter soil auger to dig down to the ground water. To find the distance, I either used a weighted

water sensor whose LED lit upon contact with water, or, for depths less than 30 cm, a ruler. Marsh soils on the barrier islands often have a thick muck layer, and those under shrubs a tight duff layer. To account for this difference, I measured water table depth as the depth from the top of the mineral horizon. Over two days in summer 2004, I used a portable conductivity meter to test water samples taken from bore holes for salinity and pH. For the next two years, I used soil salinity and pH data as determined by the soil testing lab at Virginia Polytechnic Institute and State University (VPI) (Mullins and Heckendorn 2006).

In addition to sampling as described above during vegetation surveys, during summers, I periodically checked water levels at as many pimples as possible, as dictated by rain and drought events. I did this in combination with inspection of water table data from automated water table wells installed on the island in order to get a reasonable measure of maximum and minimum water levels during the study.

*Environmental measurements: edaphic parameters*

To sample surface soil for a transect, I used a soil corer made from a plastic syringe with the end cut off to take three 15 cm<sup>3</sup> cores at the ends and middle of the transect. The three cores were mixed together for analysis to produce an average composite soil sample for the transect and stored in Whirl-Pak™ sterile sample bags (Nasco Co.). I used a soil auger to sample soil at depths determined by examining the soil profile for changes in color, an indication of redox potential and water table position (Brown et al. 1990, Huggett 1998, Silver et al. 1999, Brady and Weil 2002). Hayden et al. (1995) found that the soil profile under Parramore Island pimples was a homogeneous sand horizon. After performing a particle size analysis on twenty samples from different

depths in the dunes, I found that, regardless of depth, the soil profile in Hog Island pipples was composed of a well-sorted fine sand. A mean 92% of each sample was in the particle size range of 2-3  $\phi$  (125 – 250  $\mu\text{m}$  diam.). Particle size therefore was not useful in discriminating microhabitats, and I did not use it in analyses.

Both the depth of the organic horizon and the amount of organic matter in the mineral horizon of the soil were variable, however. These two factors are important in sandy soils for water and nutrient retention, and were therefore recorded. Soil organic matter was determined by mass loss on ignition. Depth of the organic layer was determined by observing excavated bore holes; there was typically a distinct interface between organic matter and sand.

During spring and summer 2005 and summer 2006, I collected samples for chemical analysis at the VPI soil testing laboratory. The routine battery of tests from the lab assessed levels of P, K, Ca, Mg, Zn, Mn, Cu, Fe, B, cation exchange capacity (CEC), Ca saturation (CaSat), Mg saturation (MgSat), K saturation (KSat), organic matter in the mineral (A) horizon from mass lost on ignition (OM), pH and salinity (Mullins and Heckendorn 2006). During the same collections in summer 2005 and 2006 and during spring 2006, I collected samples for  $\text{NH}_4^+$  ( $\text{NH}_4$ ) and  $\text{NO}_2^- - \text{NO}_3^-$  ( $\text{NO}_x$ ) analysis, but the 2005 sample could not be used. Within the day I collected them, I extracted the samples with a 2N KCl solution and froze them in Whirl-Pak bags to await analysis. I determined  $\text{NH}_4^+$  and  $\text{NO}_x$  levels colorimetrically on a Lachat analyzer in the Department of Environmental Sciences at the University of Virginia. Subsamples of soil collected for N analysis were air and subsequently oven dried to determine gravimetric water content.

These measurements served both as environmental parameters and as standards for KCl-extracted samples to determine actual ion content in soil.

### *Statistical analyses*

One ordination method expressly designed to relate assemblage composition to environmental factors is canonical correlation analysis or CCA (Kent and Ballard 1988, Kourtev et al. 1998). This multivariate ordination technique uses a species abundance matrix to determine multidimensional correlations among species. Mutually orthogonal axes (usually two or three) are created that describe a percentage of variation either among transects or in species' abundances, and vectors representing environmental factors are overlaid on them (Gauch 1982a, 1982b, Kent and Ballard 1988). The 'spatial' relationship between transects or species with environmental factors in ordination space represents the influence of those factors. Assumptions of CCA are multivariate normality, linear relationships between variables (i.e., CCA is a multiple multiple regression), and orthogonality of environmental factors (Gauch 1982a, Økland 1996). Multivariate normality is difficult to evaluate and achieve (ter Braak 1986, Palmer 2007), but CCA is robust to less than normal data (Minchin 1987, McCune and Mefford 1999). Monte-Carlo tests can determine if axes significantly describe linear relationships within the data matrices (McCune and Mefford 1999). A presumption of CCA is that environmental factors used are meaningful and appropriate to the community being studied; it is therefore valid practice to remove unimportant or highly-correlated environmental variables and perform analyses again to improve the solution (Økland 1996). One limitation of CCA is that calculation of its distance matrix (ordination solution) can

exaggerate contributions from rare species (Faith et al. 1987, Minchin 1987, Økland 1996).

Alternatively, multiple ANOVA's, MANOVA's, or regressions could be used to provide a complimentary analysis of the data. Although they may be helpful in *a posteriori* evaluation of single species responses, ANOVA's and MANOVA's have neither robustness against data sets with many zeroes nor the ability to evaluate relationships between all species and environmental gradients simultaneously (ter Braak 1986, McCune and Mefford 1999). Single or stepwise linear regressions are similarly insufficient compared to multivariate, multidimensional approaches (Pausas and Austin 2001). This makes CCA a more appropriate test for examining all factors simultaneously. (ANOVA analyses of habitat and location differences in edaphic factors are nevertheless included here.)

Although canonical correspondence analysis does have the attractiveness of being a direct-gradient test as opposed to ordinations based on pure statistical distance, it explains less variation in a data matrix than indirect-gradient ordinations (Minchin 1987, Kent and Ballard 1988, Økland 1996, McCune and Mefford 1999, Palmer 2007). In practice, cumulative percent variation described by the first three axes of a CCA ordination are often in the range of 20 % – 40 % (2001). In contrast, an indirect method like non-metric multidimensional scaling, which is optimized either manually or with an 'auto pilot' algorithm, often explains > 80 % of data variation in the first 1–3 axes (McCune and Mefford 1999, Palmer 2007, personal observation). This should not detract from using CCA, however. If one assumes that CCA is directly creating regression

relationships between environmental variables and species abundances, explaining 20 % – 40 % of the drivers of diversity in a community is respectable.

*Ordinations.* Because the data set is not complete for all years, all transects, and all environmental factors, I could not inspect all data together in one ordination. As such, I ran CCA analyses in two different configurations: 1) with annual mean values from all transects and a constrained set of environmental variables, and 2) with annual mean values from only pimple transects and all environmental characteristics that I recorded.

I also performed analyses with those two configurations but with matrices transposed so that I could examine relationships of species to transects and, more importantly, to environmental variables. To create a species – environmental factors matrix, I calculated mean values of each environmental variable from all transects in which a particular species occurred.

Graphical results from these ordinations will have species labeled with my arbitrary, *a priori* habit preference: xerophytic, mesophytic, or hydrophytic. I attempted to base my suppositions not only on the island habitats in which I routinely observed each species, but also on the drought tolerances and water needs those species have on the mainland. For example, I classified little blue stem, *Schizachyrium scoparium*, as mesophytic because it is typically a prairie species, even though I only found it in some of the driest dune sites on Hog Island.

In addition to CCA ordinations, I calculated non-metric multidimensional scaling analyses of both transects as well as species based on environmental variables. I performed each analysis in the two configurations described above. I wanted to compare performance of a direct-gradient approach (CCA) to an indirect approach (NMS).



## RESULTS

### *Comparison of environmental factors by habitat type*

Many environmental factors were significantly different between habitat types. There was often a difference in soil mineral content between marsh and the other habitats; this could be attributed to loss by leaching in shrub and summit zones (Fig. 20). Possibly because there was so little nitrogen in general, there was no significant pattern in nitrogen distribution, except for significantly higher nitrate–nitrite levels in main dunes versus pimples (Fig. 21). Depth of water table differed between habitat zones as well as between pimple and main dune (Fig. 21).

Since some of the distribution patterns of edaphic factors were similar, I calculated Pearson's correlation coefficients for all environmental factors (McCune and Mefford 1999). These coefficients are on a scale from 1 to -1 and measure the degree of linear relationship between variables. Boron, calcium, and magnesium were highly correlated with each other and with cation exchange capacity, but not with salinity. Copper, zinc, and phosphorus were all correlated with each other 50–70 %. Many of those minerals had either a positive correlation with water table depth that was greater than 50 %, a negative correlation with elevation that was less than -50 %, or both. Iron was correlated with organic matter content. Ammonium and nitrate–nitrite were not highly correlated with any factor, including themselves.

There were fewer correlations between physical features and other factors. Elevation, depth to water table, and organic layer thickness were correlated. Water and organic horizon thickness were correlated with some mineral nutrients and cation exchange capacity.

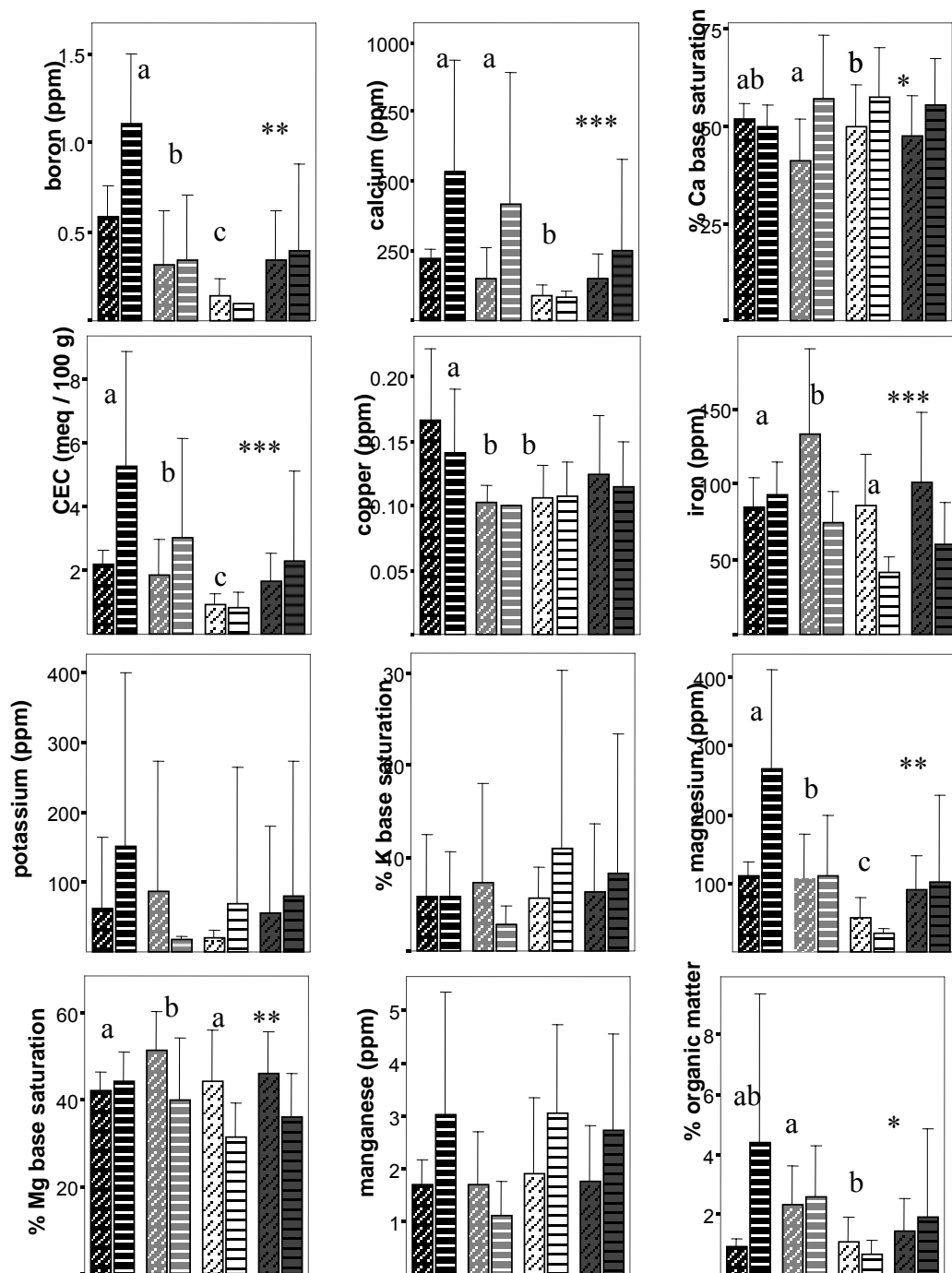


FIG. 20. Content of several nutrients, base saturations, organic matter content, and cation exchange capacity for marsh, shrub, and xeric habitat soils on pimple and main dunes. Data were analyzed with a one-way, full-factor ANOVA; letters indicate significant differences between habitats found with Tukey's multiple comparison test at  $\alpha = 0.05$ . Significant pimple-main dune effects are indicated with \* ( $p < 0.05$ ), \*\* ( $p < 0.01$ ), and \*\*\* ( $p < 0.001$ ). KEY: ▨ marsh, pimple; ▩ marsh, main dune; ▧ shrub, pimple; ▨ shrub, main dune; ▩ summit, pimple; ▧ summit, main dune; ▨ pimple total; ▩ main dune total.

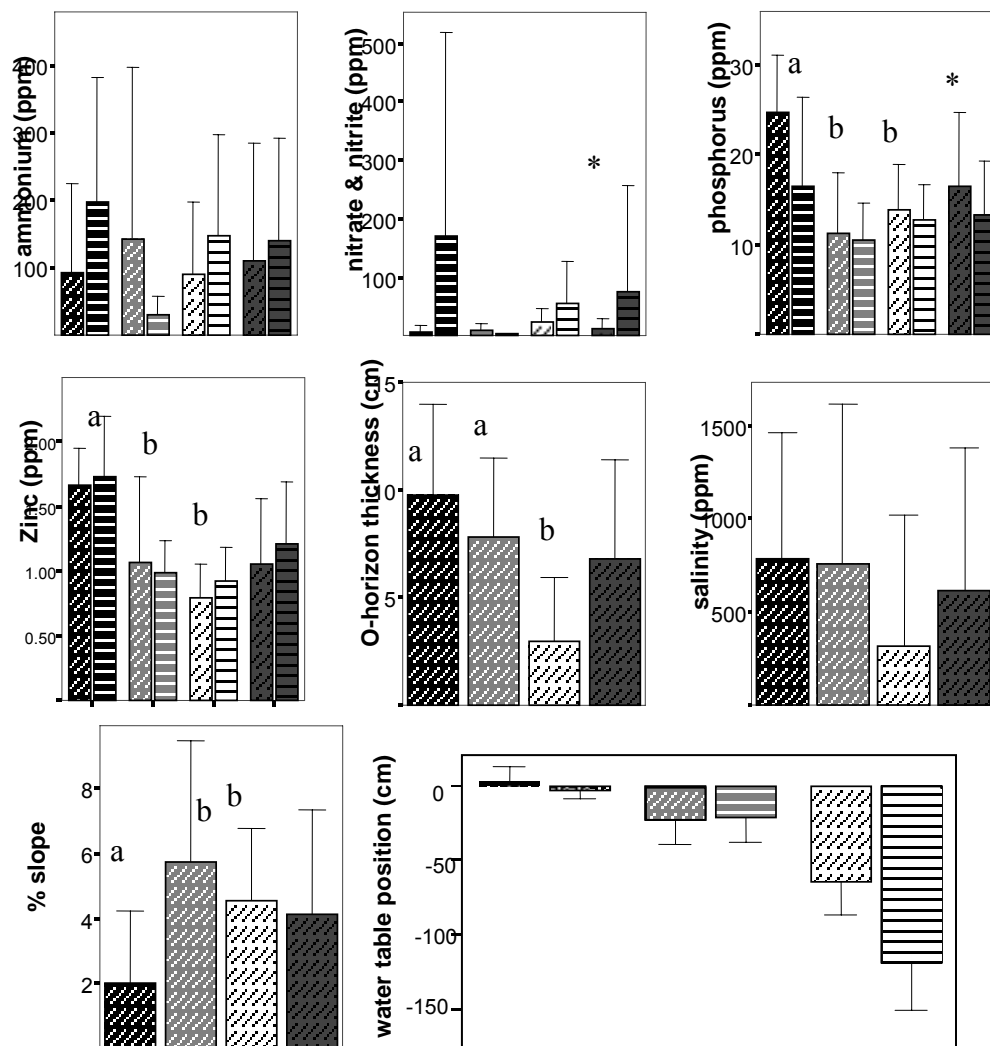


FIG. 21. Ammonium, nitrate–nitrite, phosphorus, and zinc; organic horizon thickness; salinity; % slope, and water table for three different habitats on pimples and main dunes. Data for organic horizon thickness, salinity (conductivity), and slope were only available for pimples in amounts sufficient for analysis. Data were analyzed with a one-way, full-factor ANOVA; letters indicate significant differences between habitats found with Tukey’s multiple comparison test at  $\alpha = 0.05$ . Significant pimple–main dune effects are indicated with \* ( $p < 0.05$ ), \*\* ( $p < 0.01$ ), and \*\*\* ( $p < 0.001$ ). KEY: ▨ marsh, pimple; ▩ marsh, main dune; ▧ shrub, pimple; ▦ shrub, main dune; ▨ summit, pimple; ▩ summit, main dune; ▧ pimple total; ▦ main dune total.



*Transect ordinations: combined main dune and pimple data*

Overall, total variation explained in the first three (or two) axes of non-metric multidimensional scaling ordinations was at least three times as much as in the first three axes produced by canonical correspondence analysis ordinations. Nevertheless, in every CCA ordination, all axes significantly described linear relationships between variables, i.e., the relationship between factor and transect matrices or factor and species matrices was not random (Monte-Carlo,  $P < 0.05$  for all). In every NMS ordination performed, resulting axes explained variation significantly better than would be expected by chance (Monte-Carlo test of 'stress' reduction;  $P < 0.02$  for all axes).

Canonical correspondence analysis of transects produced a solution whose first three axes together described 21.1 % of the relationship between assemblage data and environmental variables (Table 11). The ordination revealed some distinct groupings of sites based on habitat type (Fig. 22): Summit plots appeared most variable. Main dune plots were clustered more tightly than pimple plots. Habitat types sorted themselves along axis 1, which was correlated with water table depth (Fig. 23) and mineral micronutrients (Fig. 24–Fig. 27). Summit and marsh transects together segregated from shrub transects along axis 2, which was correlated with phosphorus (Fig. 28; low in shrub transects, high elsewhere) and iron (Fig. 27; high in shrubs, low elsewhere). Variation among transects within each habitat along axis 3 was correlated with nitrate–nitrite levels (Fig. 29), cation-exchange capacity (Fig. 30), and organic matter (Fig. 31).

TABLE 11. Pearson's  $r$  correlation coefficients of environmental variables for the first three axes of a CCA of main dunes and pimples and percentage of variation explained. In all subsequent tables, percentages listed with axes refer to the percent of variation explained by that particular axis.

Axis 1: 9%		Axis 2: 7%		Axis 3: 5%	
	R		r		r
water table	0.954	P	-0.675	NO <sub>x</sub>	0.887
B	0.601	Fe	0.586	CEC	0.638
Zn	0.572	Zn	-0.543	OM	0.616
Mg	0.535	MgSat	0.53	Ca	0.578
Fe	0.502	B	-0.44	Mg	0.551
MgSat	0.497	Cu	-0.436	K	0.452
CEC	0.423	CaSat	-0.431	B	0.385
Mn	-0.377	OM	0.415	MgSat	-0.348
Ca	0.371	Mn	-0.312	Zn	0.32
Cu	0.336	NO <sub>x</sub>	0.213	Mn	0.204
P	0.316	Ca	-0.121	CaSat	0.199
CaSat	-0.296	CEC	-0.072	NH <sub>4</sub>	0.184
OM	0.242	KSat	-0.069	Fe	-0.153
KSat	-0.184	K	0.052	KSat	0.137
NO <sub>x</sub>	-0.122	water table	0.038	P	0.097
NH <sub>4</sub>	-0.051	Mg	-0.027	Cu	0.091
K	0.025	NH <sub>4</sub>	0.011	water table	0.01

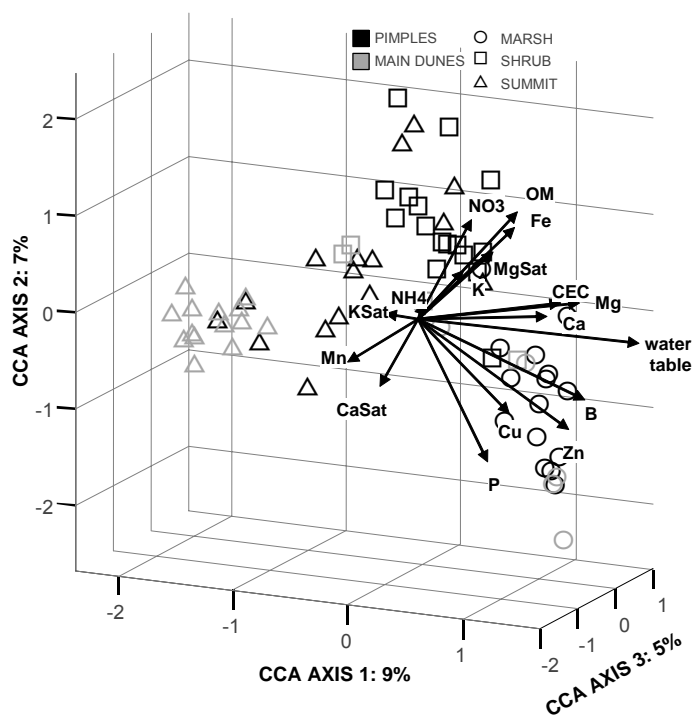


FIG. 22. Canonical correspondence analysis ordination of main dune and pimple transects. In this figure and all other CCA figures like it, lengths of environmental factor vectors have been exaggerated by a factor of two for legibility. In all other figures, percentages listed on axes refer to the percentage of variation explained.

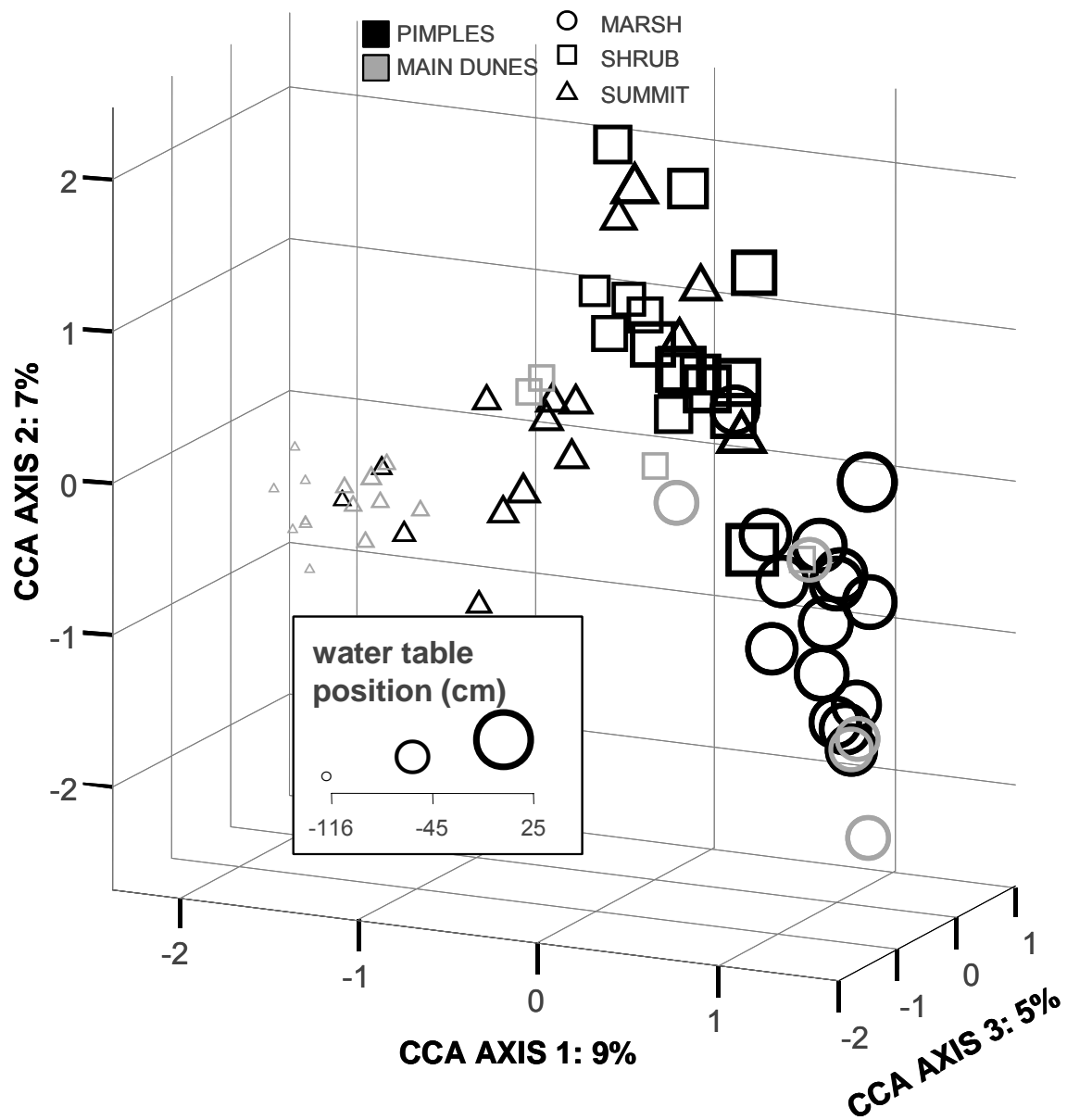


FIG. 23. Overlay of water table position on the CCA ordination of pimple and main dune transects.

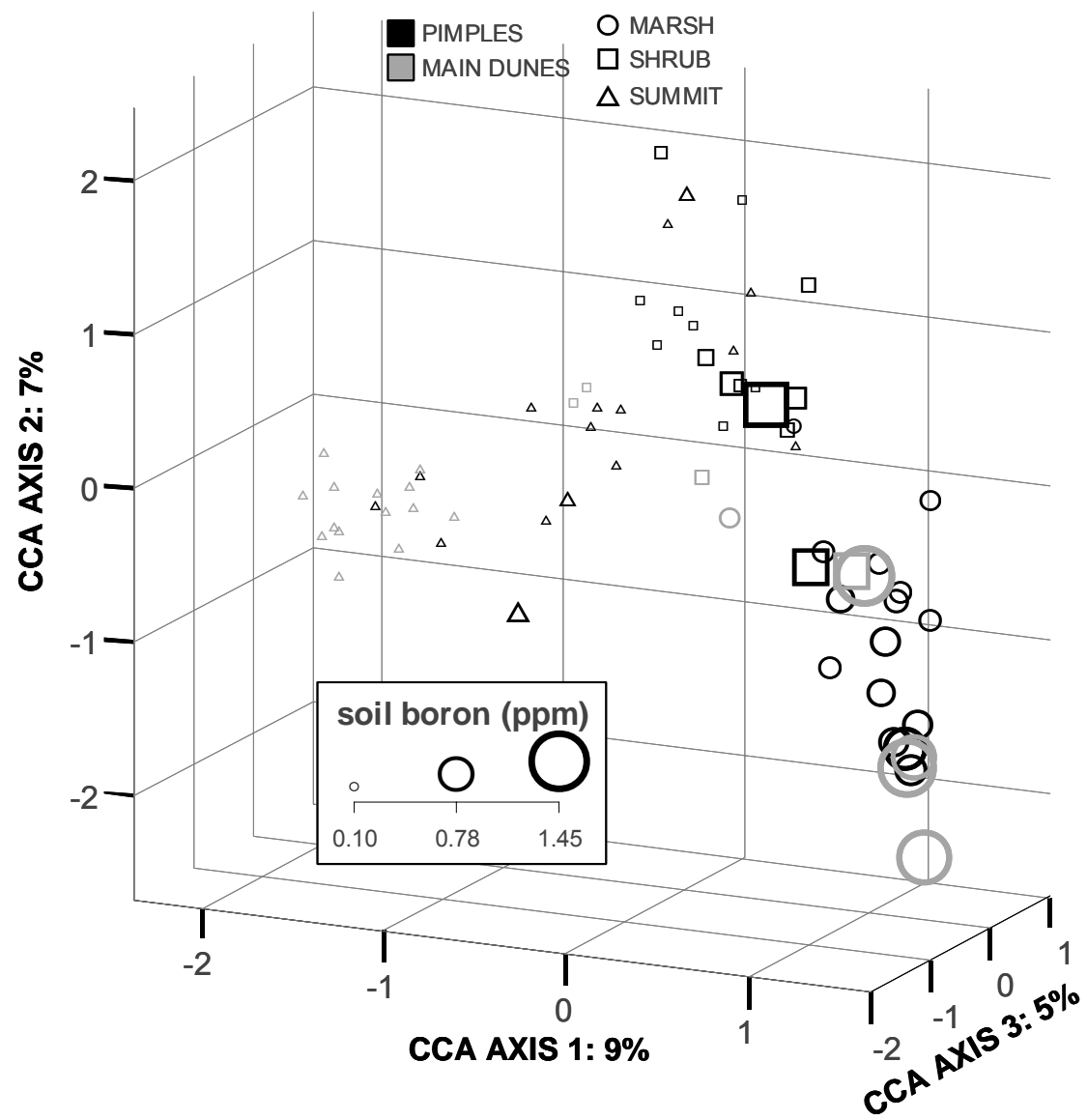


FIG. 24. Overlay of soil boron concentration on the CCA ordination of pimple and main dune transects.



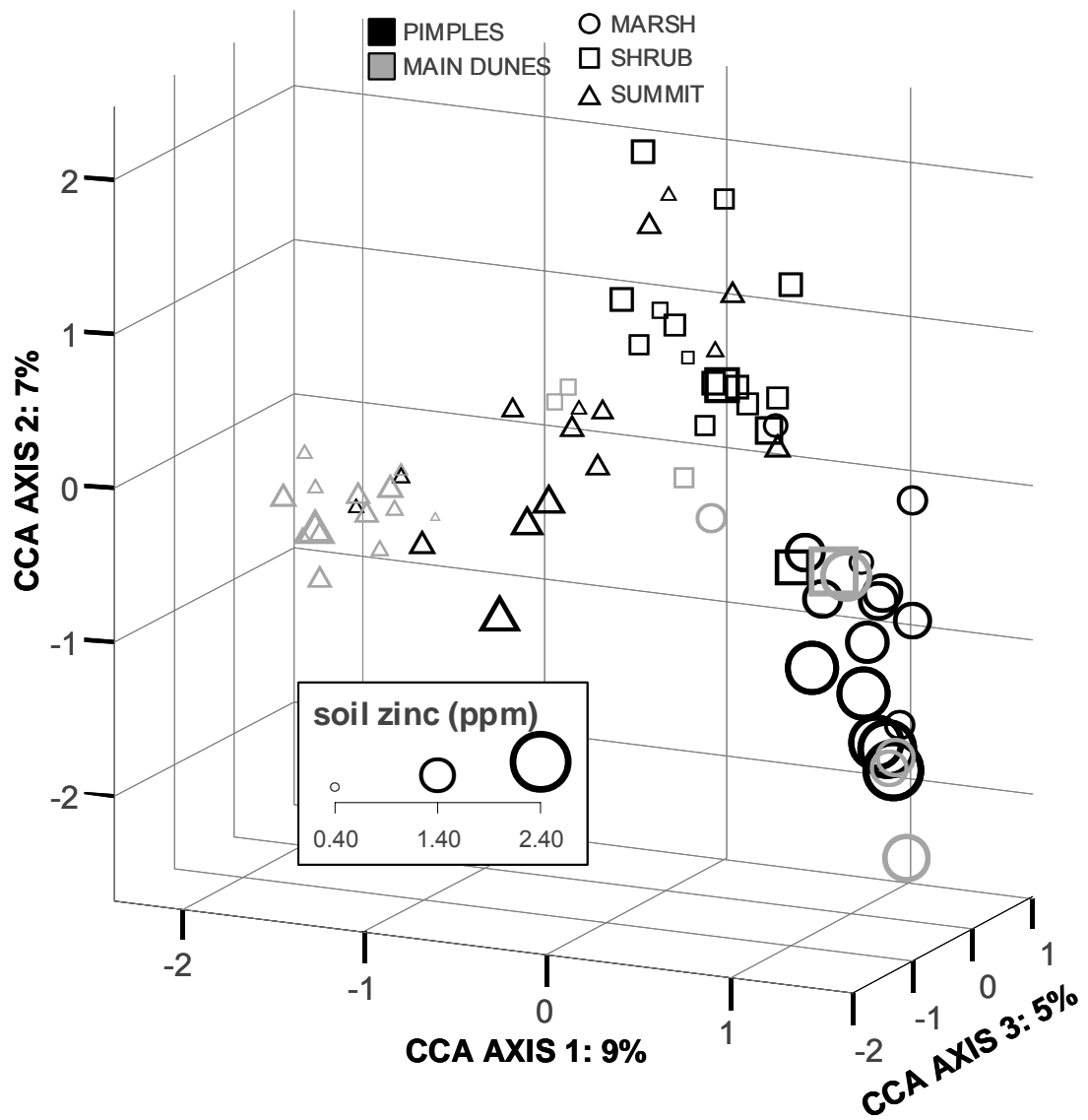


FIG. 25. Overlay of soil zinc concentration on the CCA ordination of pimple and main dune transects.

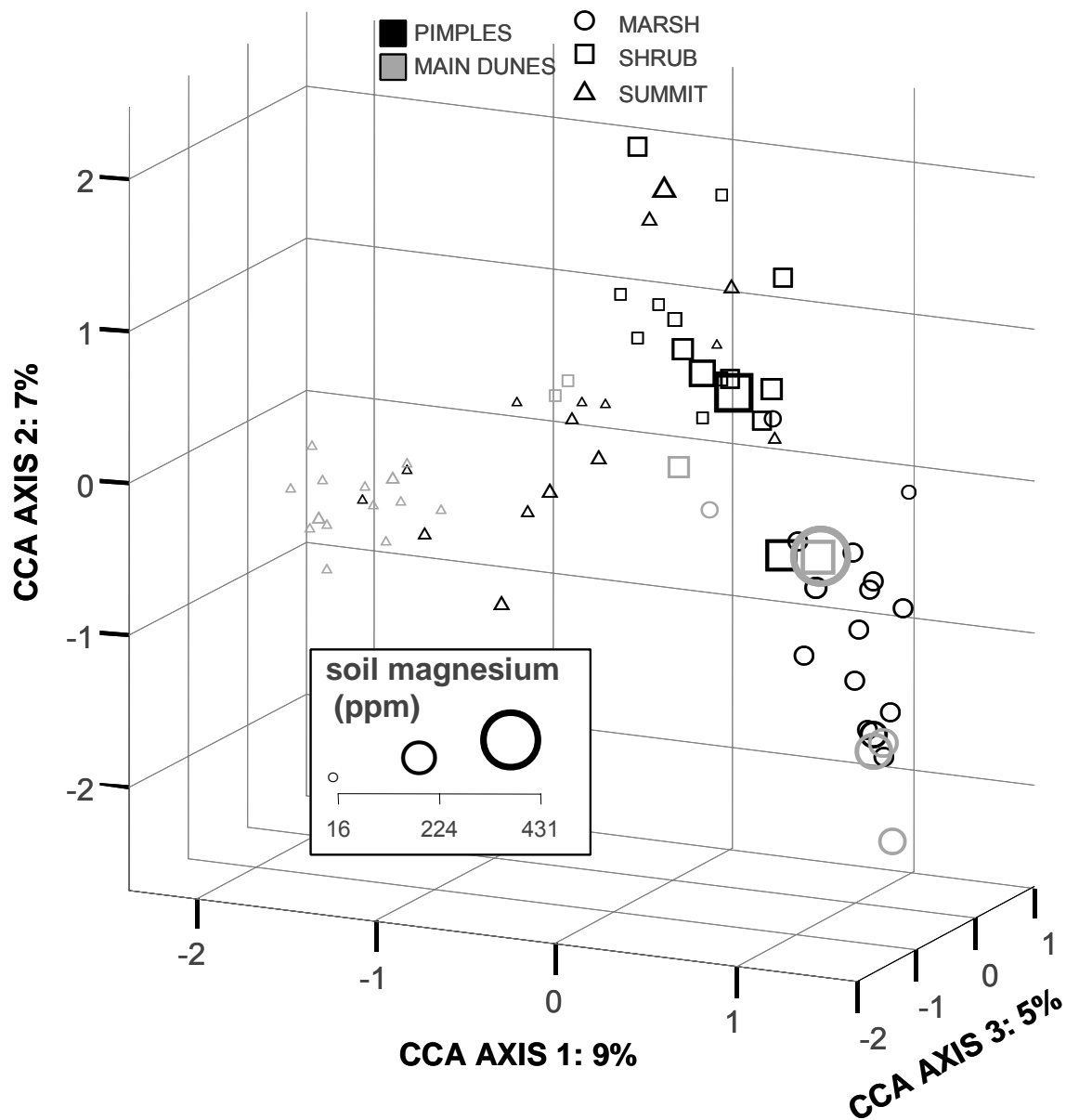


FIG. 26. Overlay of soil magnesium concentration on the CCA ordination of pimple and main dune transects.

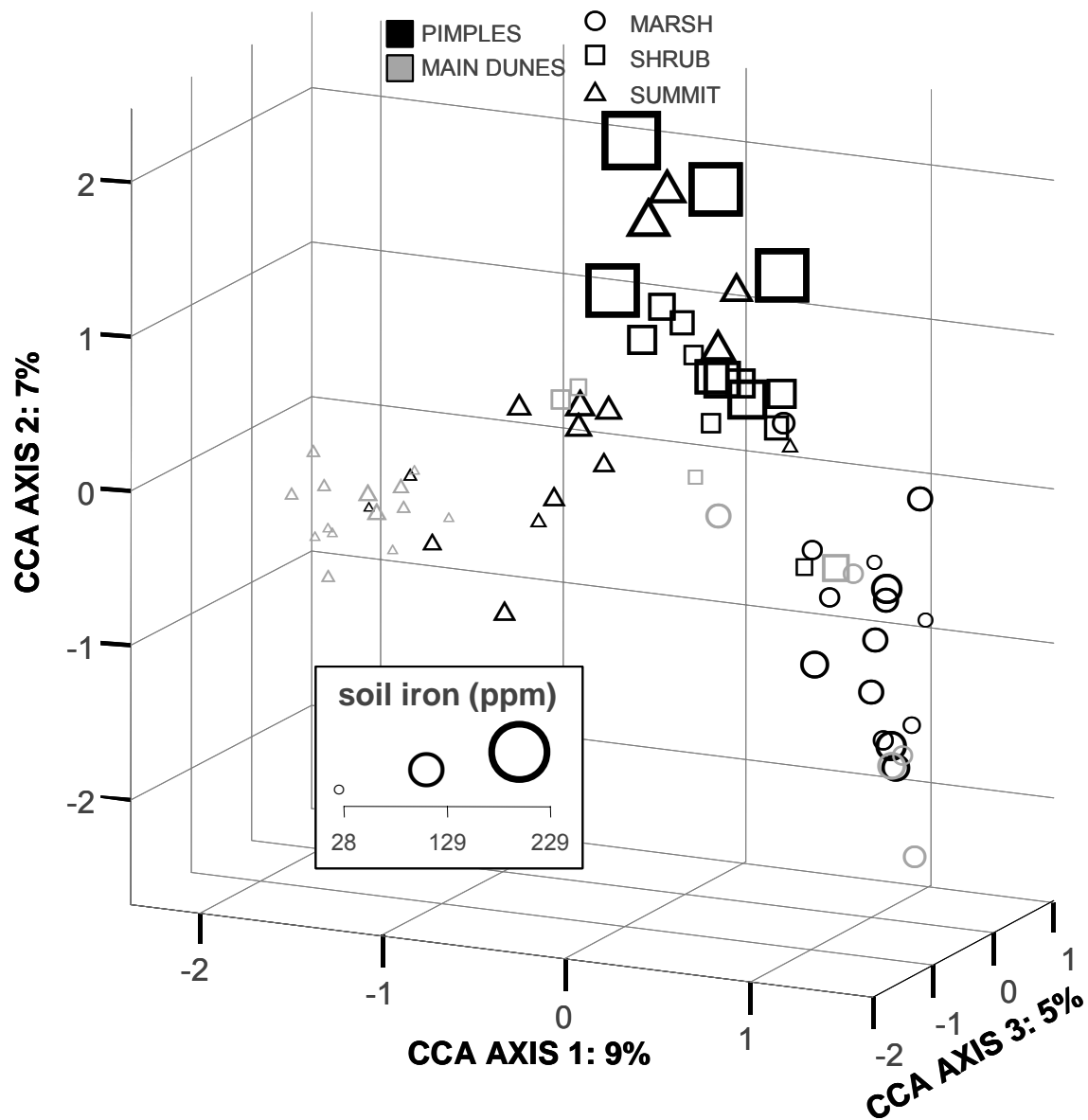


FIG. 27. Overlay of soil iron concentration on the CCA ordination of pimple and main dune transects.

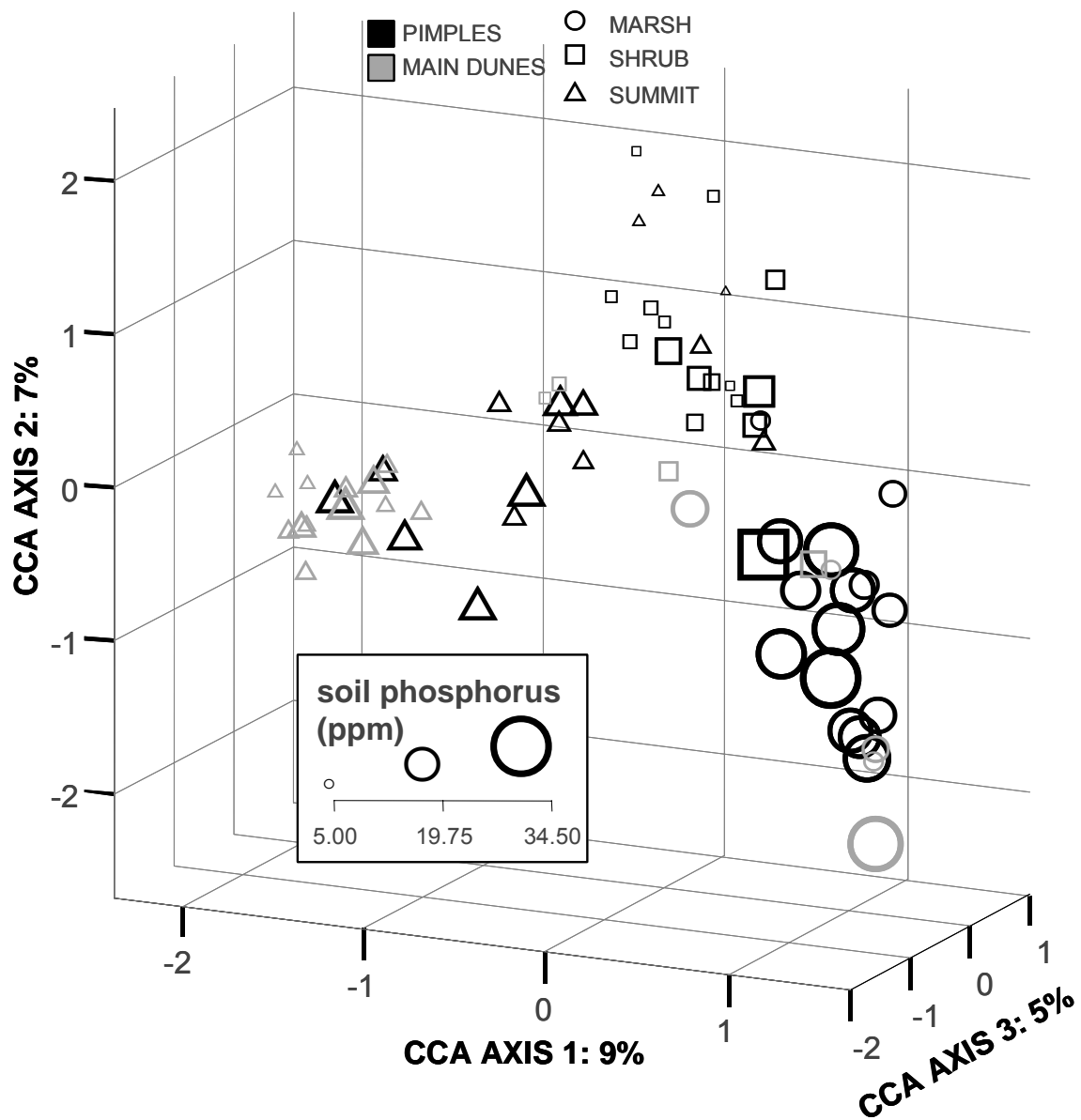


FIG. 28. Overlay of soil phosphorus concentration on the CCA ordination of pimple and main dune transects.

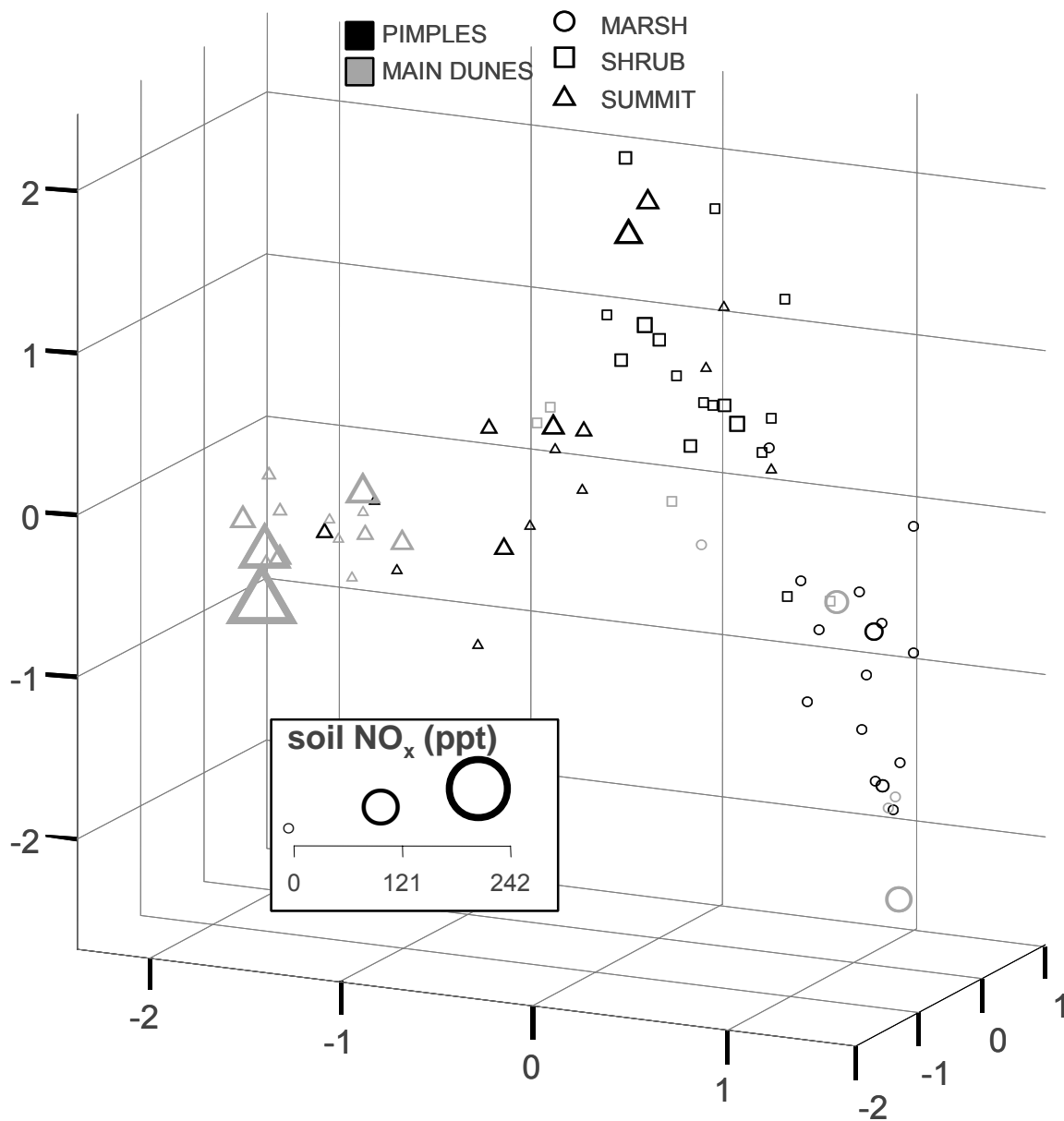


FIG. 29 Overlay of soil nitrate – nitrite concentration on the CCA ordination of pimple and main dune transects.

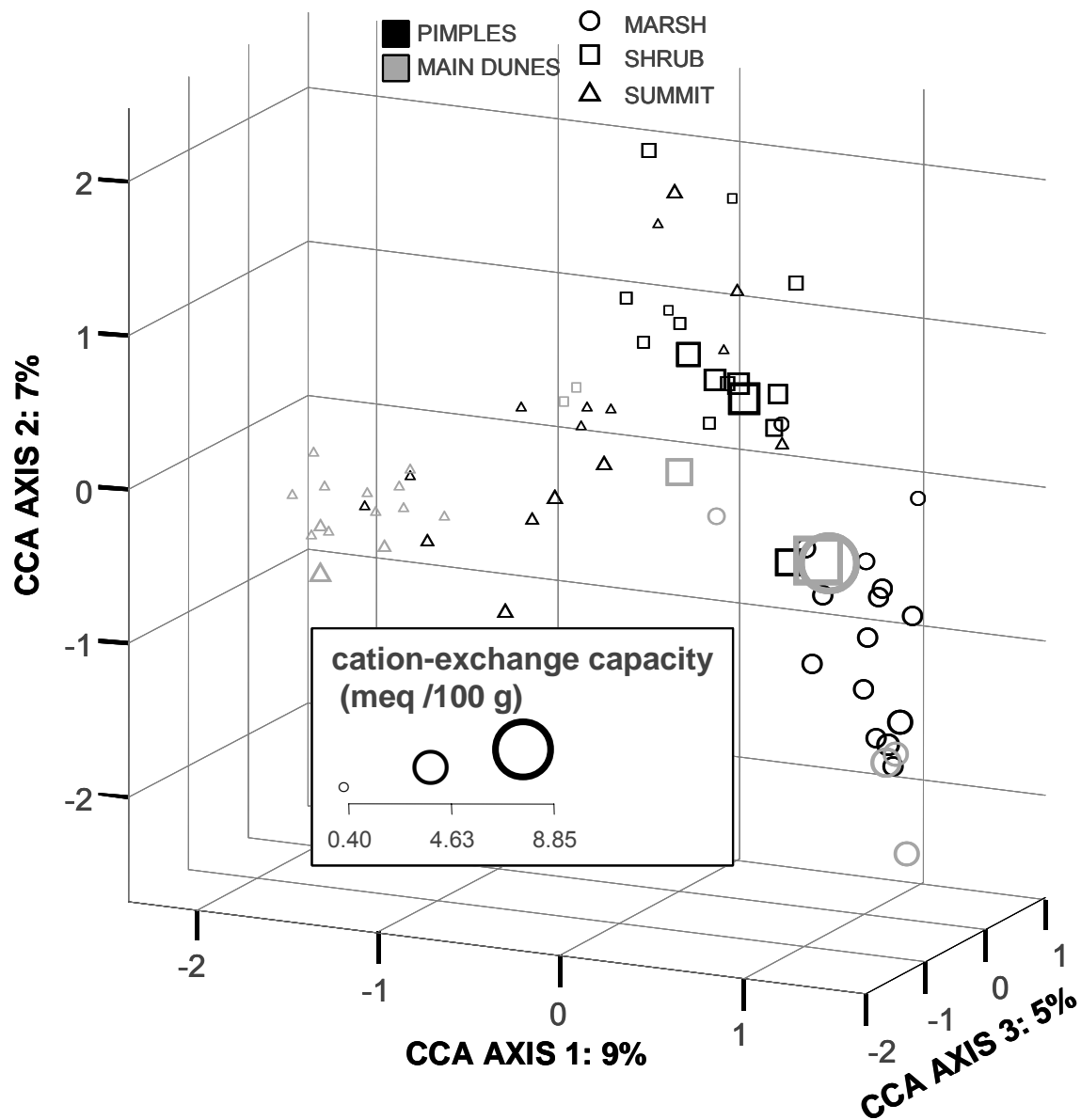


FIG. 30. Overlay of soil cation-exchange capacity on the CCA ordination of pimple and main dune transects.

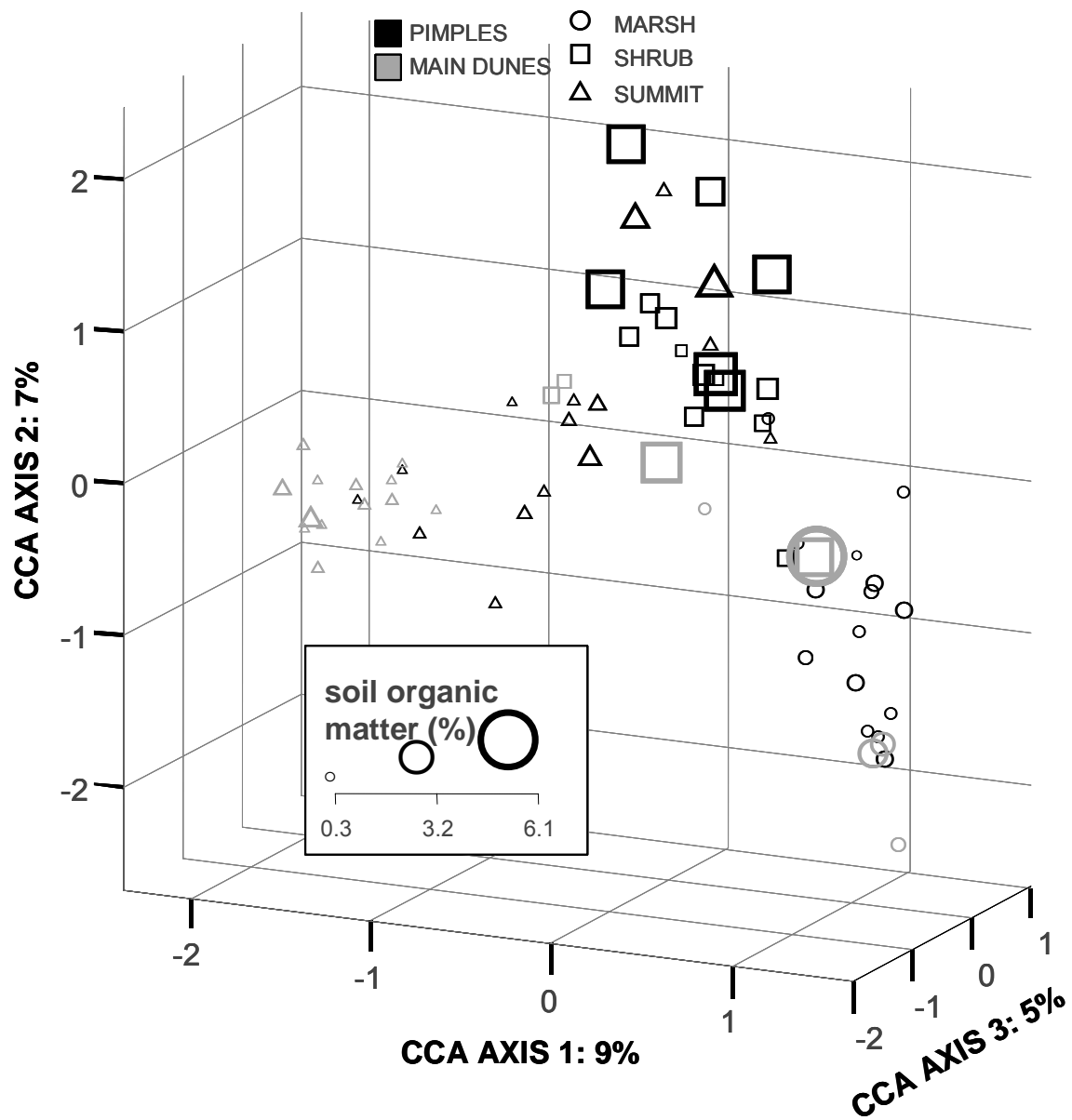


FIG. 31. Overlay of soil organic matter concentration on the CCA ordination of pimple and main dune transects.

Analysis of explanatory power changes between subsequent axes in non-metric multidimensional scaling revealed that a three-dimensional solution was optimal. The resulting three axes in the solution described 55 %, 21 %, and 20% of the variation (96 % cumulative; Table 12; Fig. 32). The two factors most highly correlated to each axis were, respectively, potassium and potassium saturation (Fig. 33), water and ammonium (Fig. 34, Fig. 35), and calcium and cation-exchange capacity.

TABLE 12. Pearson's  $r$  correlation coefficients for the three axes of a NMS solution of main dune and piñon transects versus environmental factors.

Axis 1: 55 %		Axis 2: 21 %		Axis 3: 20 %	
	$r$		$r$		$r$
KSat	-0.674	water table	-0.608	Ca	0.736
K	-0.612	NH <sub>4</sub>	0.477	CEC	0.693
NH <sub>4</sub>	-0.543	CEC	-0.45	MgSat	-0.608
CaSat	0.48	K	-0.448	B	0.592
NO <sub>x</sub>	-0.344	Mg	-0.433	Mg	0.583
Cu	0.216	CaSat	0.418	CaSat	0.512
P	0.214	Zn	-0.406	Mn	0.497
OM	-0.15	B	-0.402	Fe	-0.475
Zn	0.145	Ca	-0.33	NH <sub>4</sub>	0.433
MgSat	0.143	Mn	0.299	Zn	0.403
Mn	-0.105	Fe	-0.297	NO <sub>x</sub>	0.337
water table	0.087	KSat	-0.274	P	0.326
Ca	0.091	Cu	-0.259	OM	0.275
CEC	-0.084	OM	-0.244	K	0.232
Fe	-0.045	P	-0.216	Cu	0.182
B	0.047	MgSat	-0.18	KSat	0.061
Mg	-0.013	NO <sub>x</sub>	0.026	water table	-0.014

*Summary.* CCA and NMS found different patterns in the transects. CCA, based on linear relationships between factors and transects found water availability and cationic minerals to be the most important factors for discriminating groups of transects. NMS, which finds the optimal solution for describing differences between transects focused more on potassium and ammonium but otherwise found similar groupings to CCA.



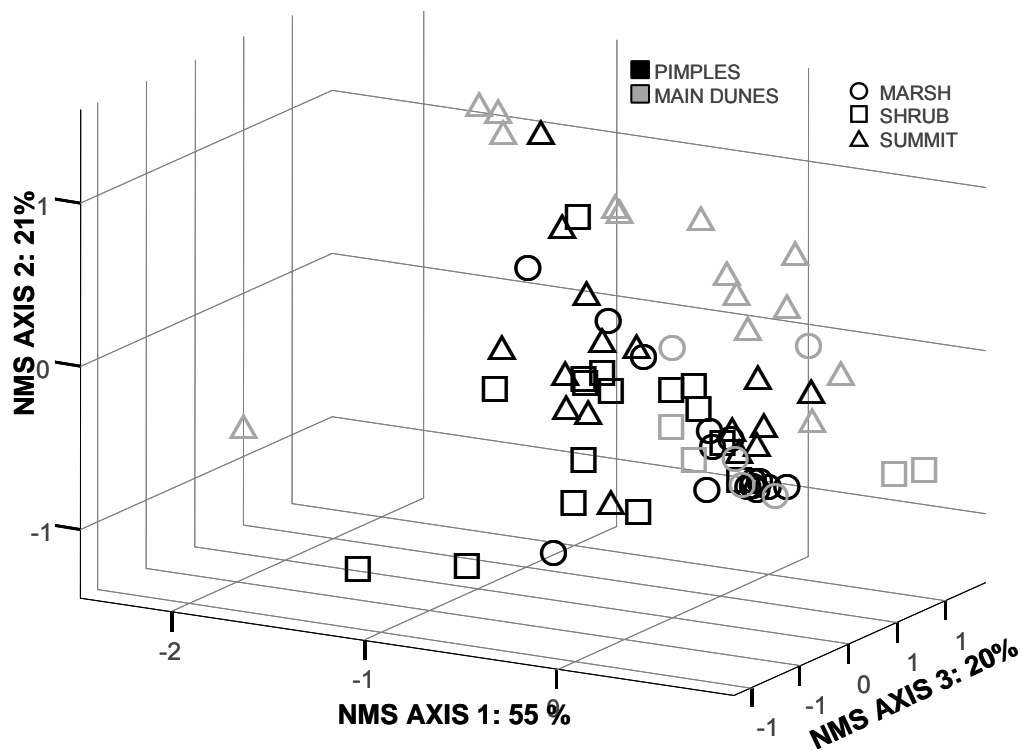


FIG. 32. Non-metric multidimensional scaling ordination of pimple and dune transects based on environmental factors.

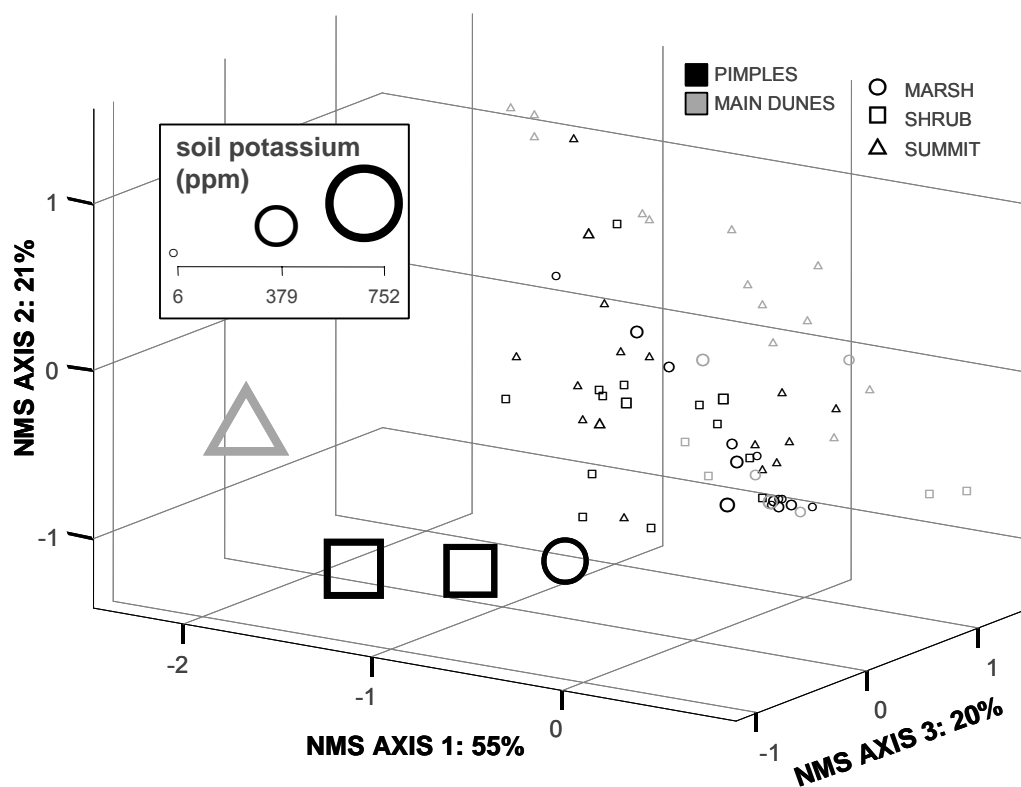


FIG. 33. Overlay of potassium concentration on pimple and dune transects in a non-metric multidimensional scaling ordination.

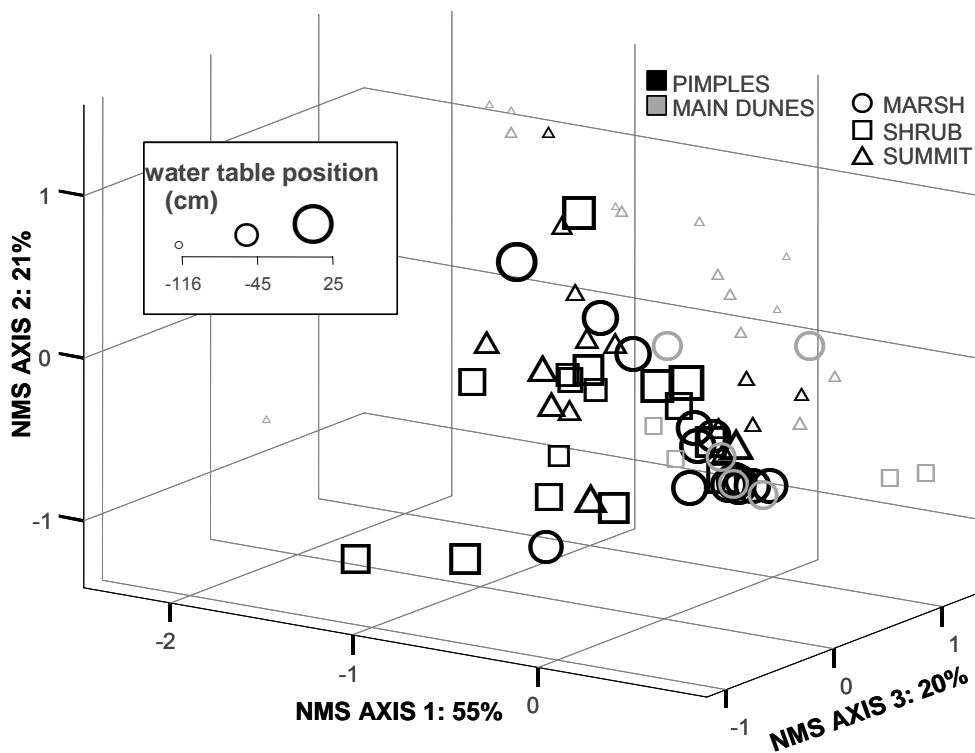


FIG. 34. Overlay of water table height on pimple and main dune transects in a non-metric multidimensional scaling ordination.

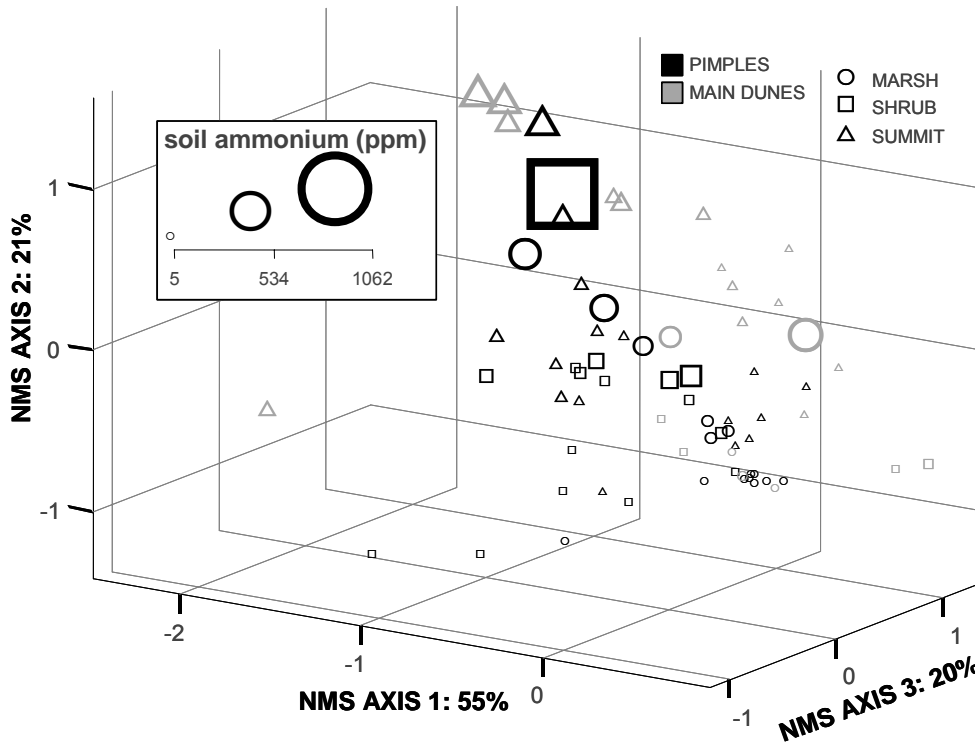


Fig. 35. Overlay of soil ammonium concentration on pimple and dune transects in a non-metric multidimensional scaling ordination.

*Transect ordinations: pimples with all recorded environmental factors*

Canonical correspondence analysis of the transect species abundances versus transect environmental variables for pimples described 31 % in the first three axes of the solution (Table 13). This was an improvement over CCA ordination with both main dune and pimple transects. Axis 1 represented an elevation – water table gradient (Fig. 37 & Fig. 38). Axis 2 was correlated with magnesium (Fig. 39) and cation-exchange capacity (Fig. 40). Axis 3 was correlated with phosphorus, magnesium saturation, organic matter, and iron (Fig. 41–Fig. 42).

TABLE 13. Pearson's  $r$  correlation coefficients for three axes of a CCA solution describing the relationship between pimple transect assemblages and environmental factors.

Axis 1: 12 %		Axis 2: 10 %		Axis 3: 9 %	
	$r$		$r$		$r$
elevation	0.906	Mg	-0.434	P	-0.795
water table	-0.901	CEC	-0.406	MgSat	0.694
o horizon	-0.784	Ca	-0.306	OM	0.646
CEC	-0.54	salinity	-0.304	Fe	0.621
B	-0.534	OM	-0.295	Zn	-0.597
Mg	-0.527	NH <sub>4</sub>	0.295	CaSat	-0.589
Ca	-0.482	B	-0.27	Cu	-0.463
Zn	-0.425	water table	-0.262	B	-0.456
NO <sub>x</sub>	0.354	slope	0.253	Ca	-0.412
Salinity	-0.297	elevation	0.241	slope	0.372
Mn	0.246	Cu	-0.238	CEC	-0.223
P	-0.237	CaSat	0.24	Mn	-0.207
Cu	-0.222	MgSat	-0.217	NO <sub>x</sub>	0.141
Fe	-0.215	Zn	-0.208	salinity	0.139
K	-0.189	Fe	-0.176	water table	-0.121
CaSat	0.166	K	-0.162	elevation	0.12
slope	0.157	Mn	0.151	east	0.116
MgSat	-0.154	P	-0.145	o horizon	0.109
OM	-0.147	north	0.128	KSat	-0.063
East	-0.081	KSat	-0.058	Mg	-0.023
North	-0.084	o horizon	-0.041	NH <sub>4</sub>	0.021
NH <sub>4</sub>	-0.077	east	0.038	K	-0.016

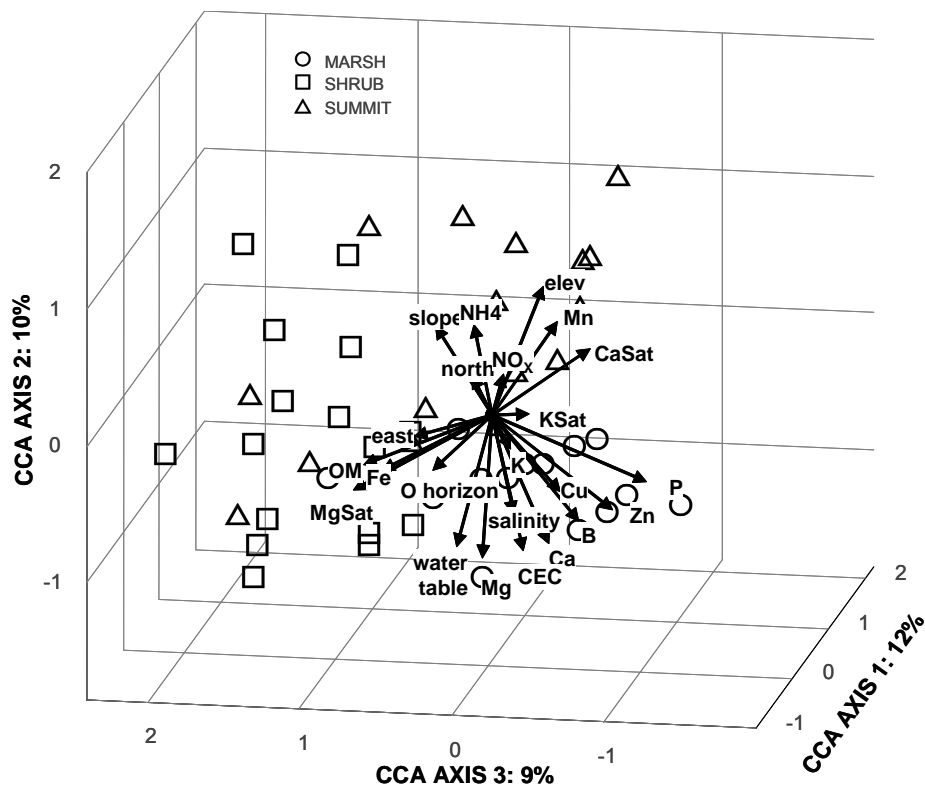


FIG. 36. Canonical correspondence analysis of pimple transects with all recorded environmental variables.

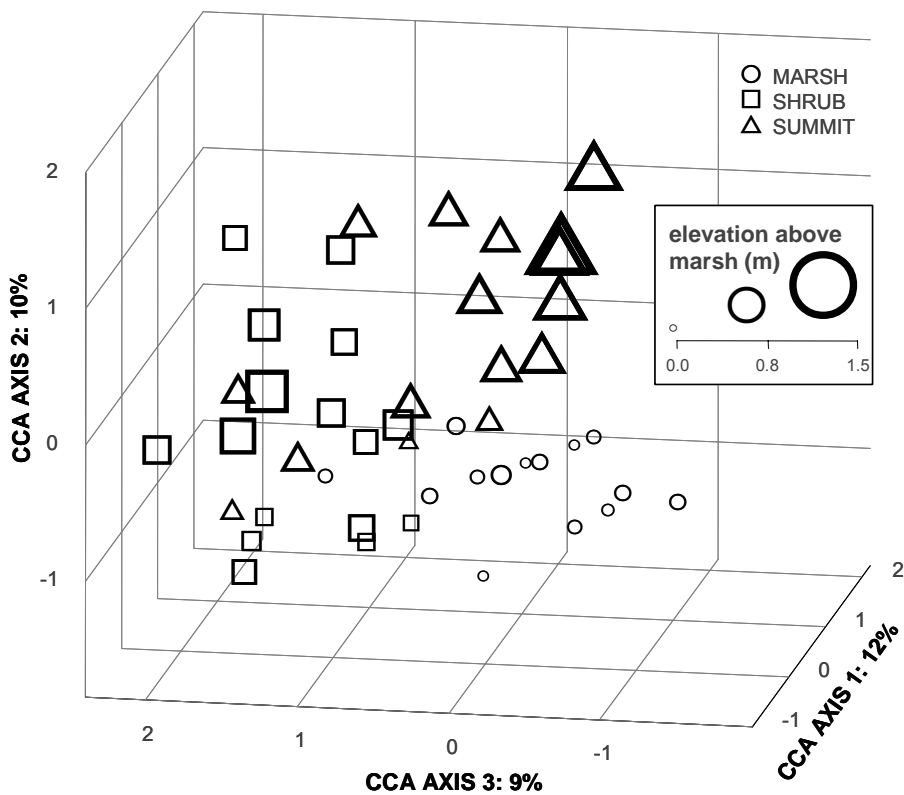


FIG. 37. Overlay of elevation above marsh on a CCA of pimple transects.

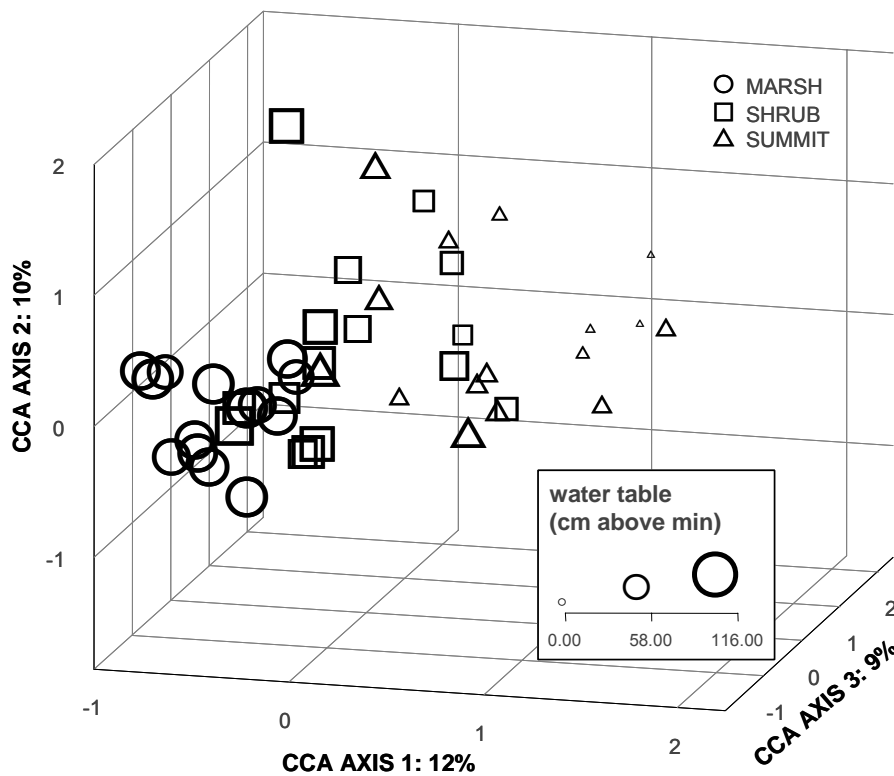


FIG. 38. Overlay of water table position above the mean minimum level on a CCA of pimple transects.

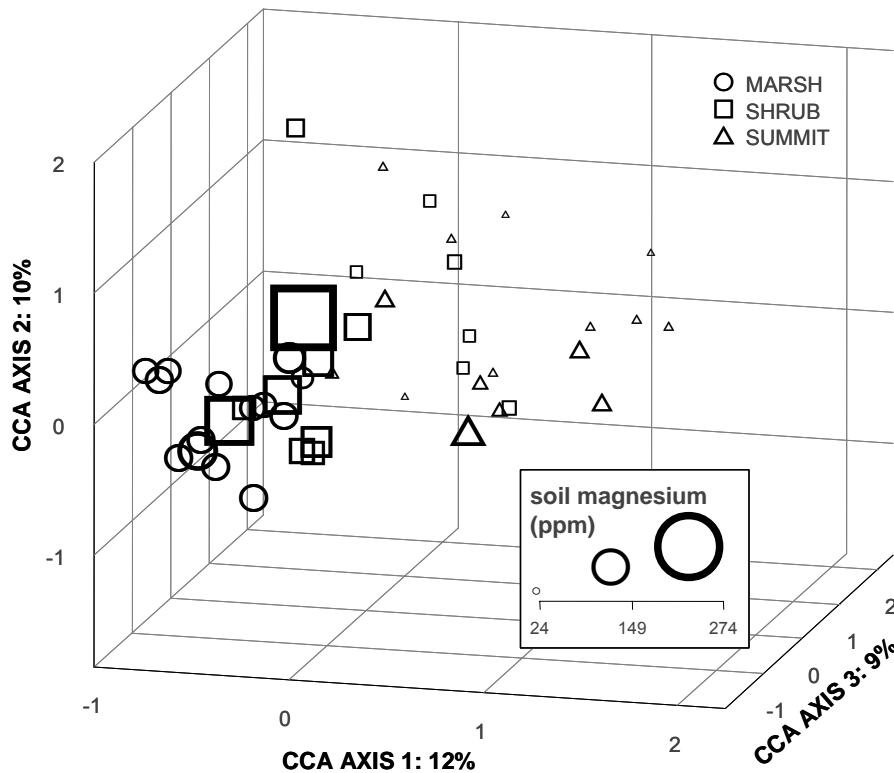


FIG. 39. Overlay of soil magnesium concentration on a CCA of pimple transects.

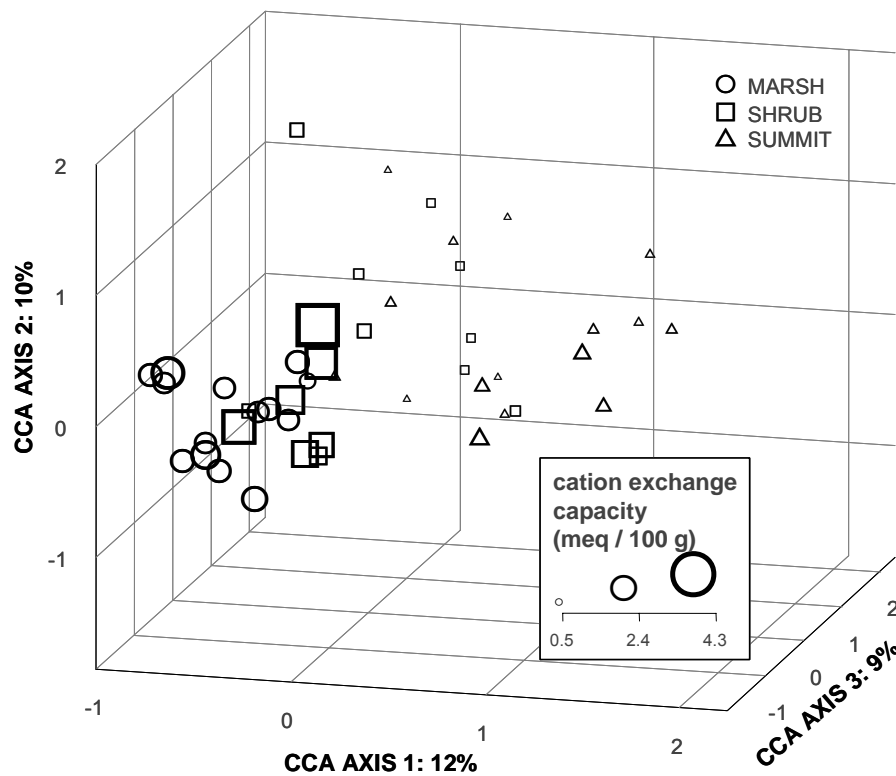


FIG. 40. Overlay of cation-exchange capacity on a CCA of pimple transects.

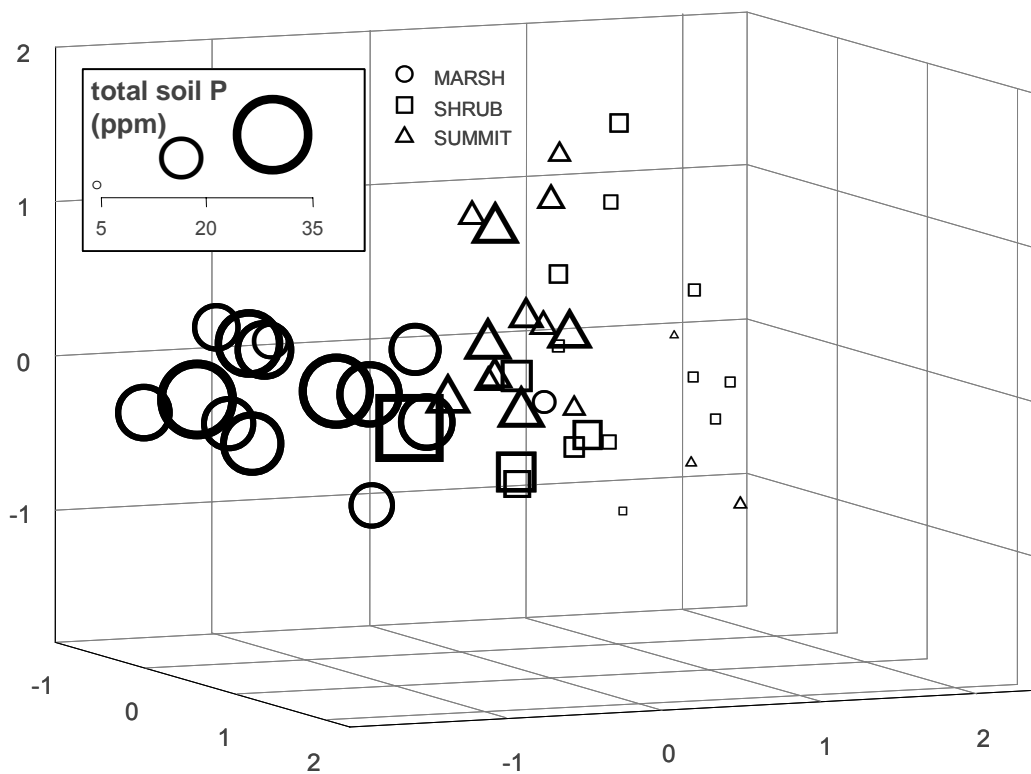


FIG. 41. Overlay of soil phosphorus concentration on a CCA of pimple transects.

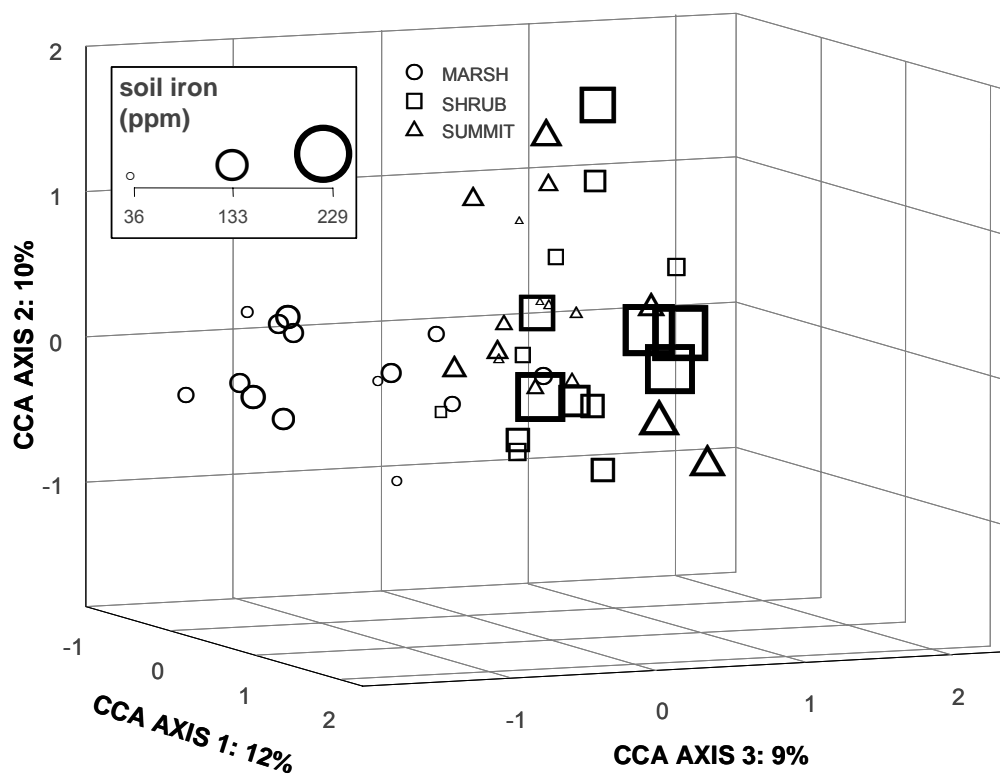


FIG. 42. Overlay of soil iron concentration on a CCA of pimple transects.

A two-dimensional non-metric multidimensional scaling solution described variation best, with the axes explaining 47 % and 48 % of variation in the data (Table 14). Shrub transects were not grouped with each other as distinctly as summit and marsh transects (Fig. 43) Water table position, elevation, salinity, magnesium, and ammonium were important to defining groups of transects (Fig. 46–Fig. 48).

*Summary.* For both ordination methods, important factors in explaining variation between pimple transects were water table position, elevation above marsh, and thickness of organic horizon. Boron, calcium, magnesium and phosphorus were more important in the CCA than the NMS analysis. Salinity, ammonium, and potassium were more important in the NMS solution than in CCA ordination. Transects were more distinctly segregated by habitat in the CCA ordination than the NMS.

TABLE 14. Pearson's  $r$  correlation coefficients for two axes in a non-metric multidimensional scaling ordination of pimple transects based on environmental factors.

Axis 1: 47 %		Axis 2: 48 %	
	$r$		$R$
elevation	-0.567	salinity	-0.856
water table	0.546	water table	-0.549
NH <sub>4</sub>	-0.521	elevation	0.459
salinity	0.512	MgSat	-0.427
K	0.479	CaSat	0.408
NO <sub>x</sub>	-0.462	Fe	-0.39
o horizon	0.447	Mn	0.366
CEC	0.443	o horizon	-0.349
KSat	0.354	Mg	-0.324
CaSat	-0.351	B	-0.233
Mg	0.34	CEC	-0.219
Zn	0.324	Zn	-0.214
Cu	0.281	OM	-0.187
B	0.272	slope	0.132
Ca	0.243	Ca	-0.093
slope	-0.226	K	-0.079
P	0.205	north	0.077
Mn	-0.188	NH <sub>4</sub>	-0.06
MgSat	0.108	NO <sub>x</sub>	0.04
Fe	0.08	KSat	-0.026
north	-0.061	Cu	-0.013
OM	0.048	P	0.009

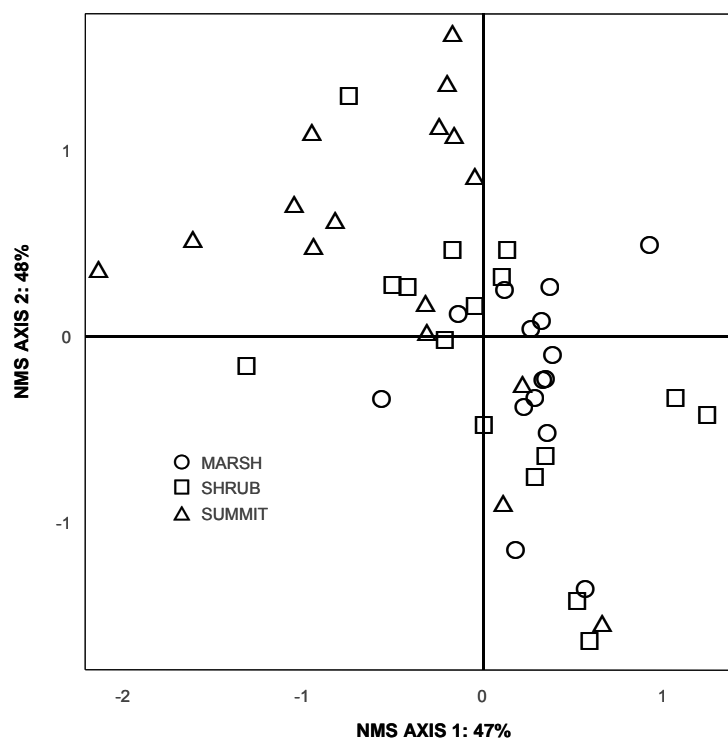


FIG. 43. Non-metric multidimensional scaling ordination of pimple transects.



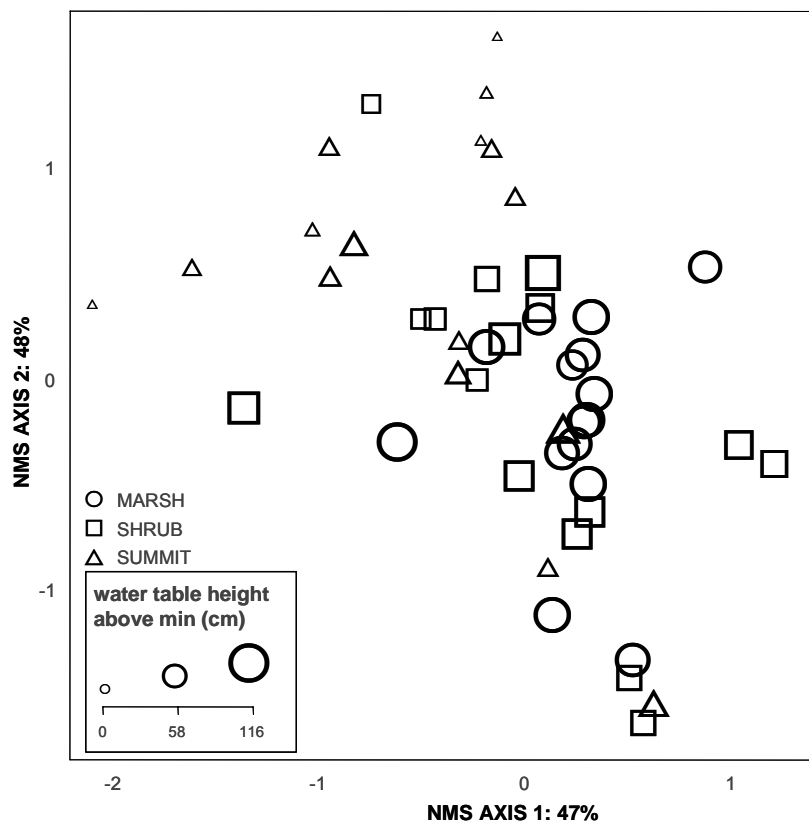


FIG. 44 Overlay of water table position on a NMS ordination of pimple transects.

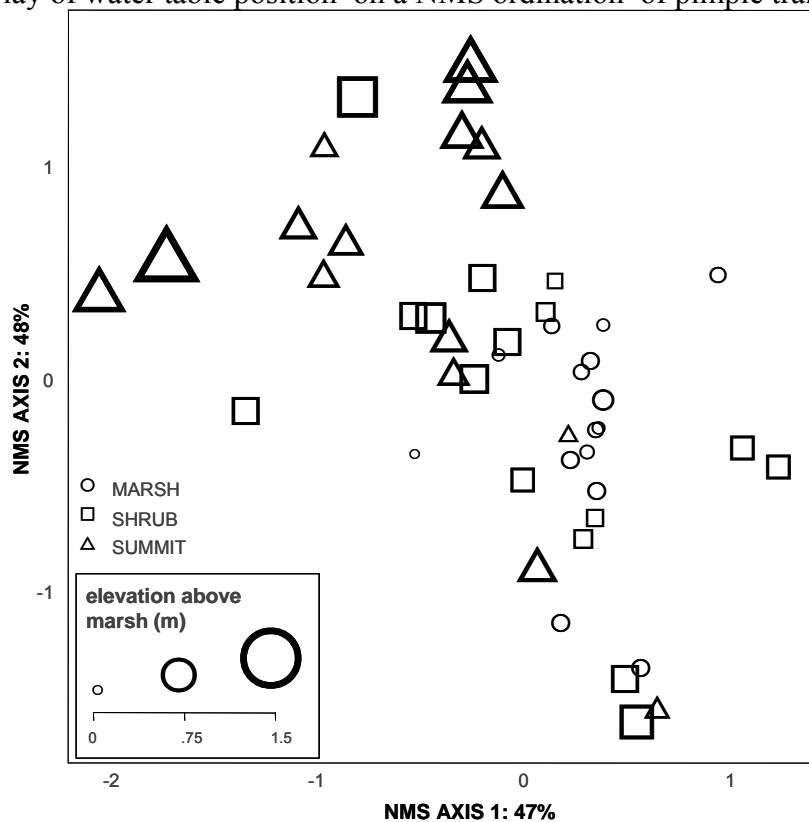


FIG. 45. Graphic overlay of elevation on pimple transects in an NMS ordination.

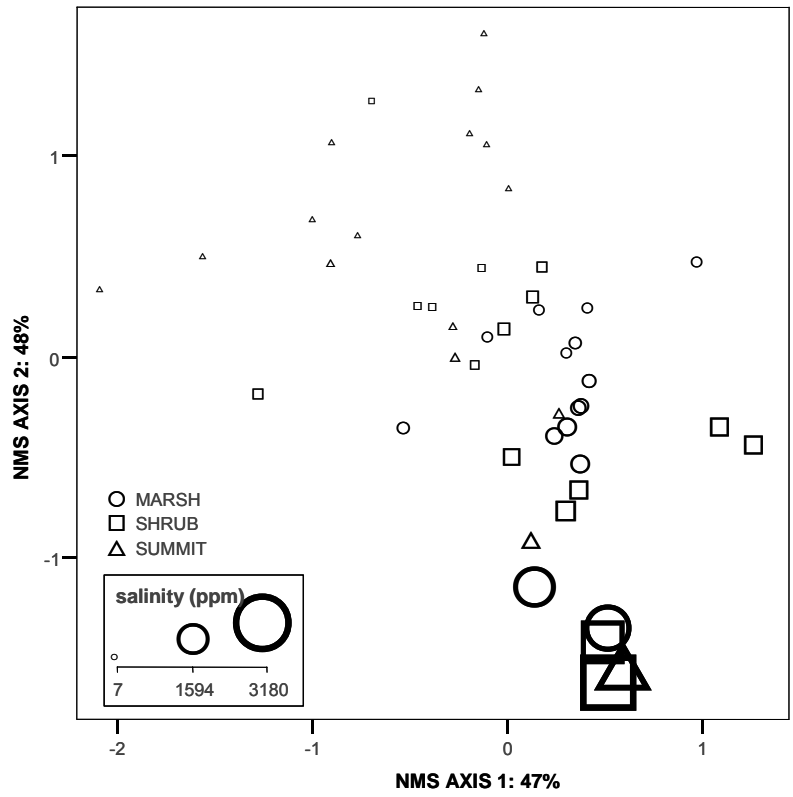


FIG. 46. Overlay of salinity on pimple transects in an NMS ordination.

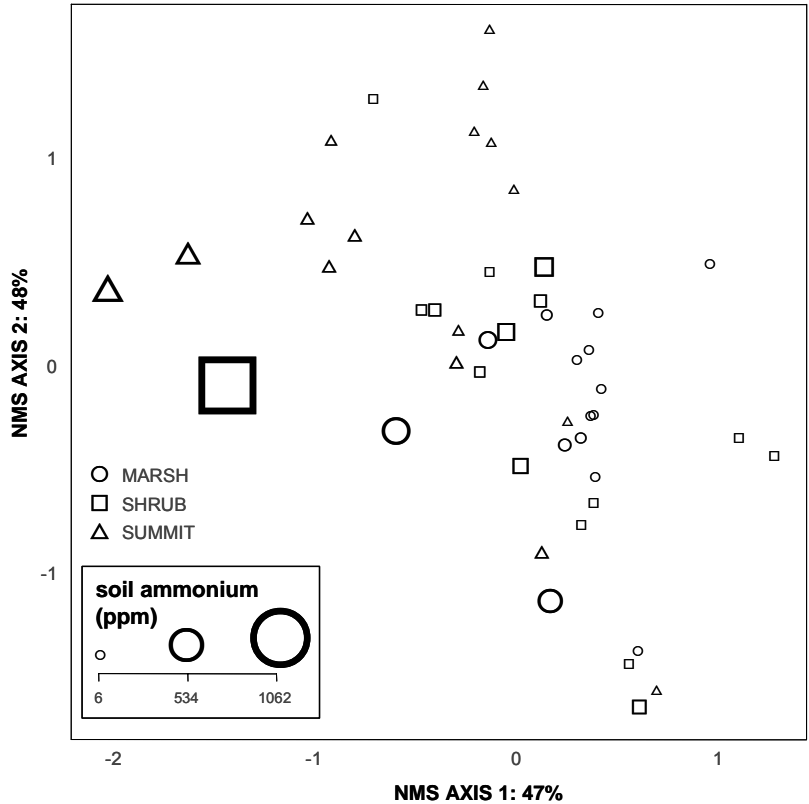


FIG. 47. Overlay of ammonium concentrations on pimple transects in an NMS ordination.

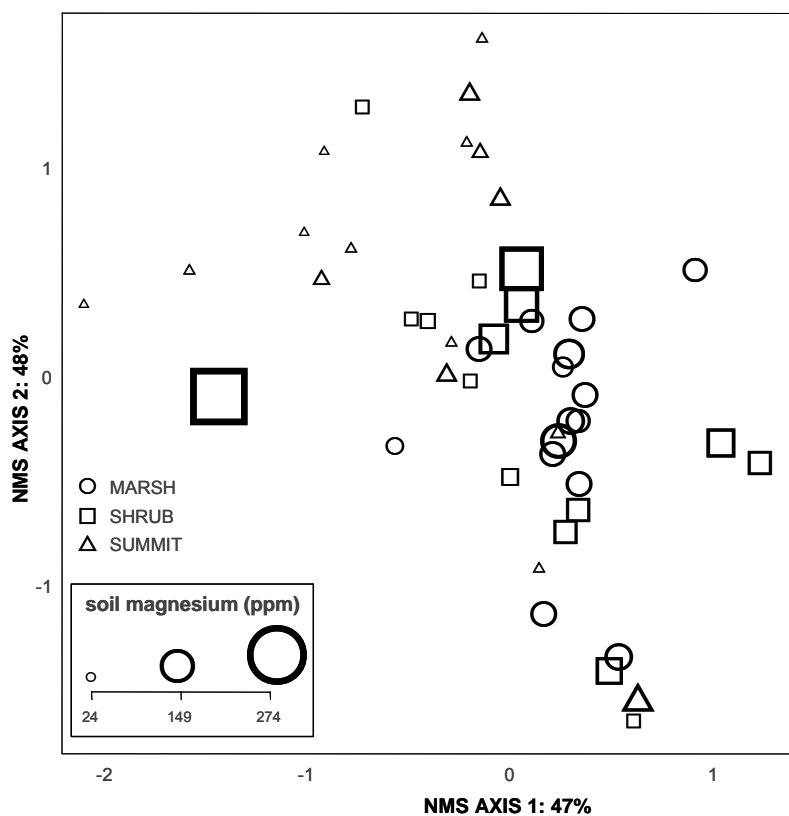


FIG. 48. Overlay of magnesium concentration on pimple transects in an NMS ordination.

*Species ordinations: species from both main dunes and pimples*

Overall, *ordinations of species* based on environmental variables (the mean from transects in which the species occurred) explained more variation than *ordinations of transects* based on environmental variables. Surprisingly, mean water table height did not have strong correlation coefficients on most major axes of most ordinations of species.

Canonical correspondence analysis of data combined from both dune and pimple species explained 26 % of variation in the first three axes (Table 15; Fig. 49). The three axes were highly correlated with boron, zinc, and magnesium; iron; and organic matter and ammonium, respectively (Fig. 50 – Fig. 55). Based on previous observation and an initial examination of the results, I tracked a few species through overlays of environmental factors on the dune and pimple CCA.

Five species represented marsh and summit flora. *Ammophila breviligulata* and *Panicum amarum* are both dominant grasses of dry dune summits. *Cyperus strigosus* and *Distichlis spicata* are representative hydrophytic graminoids. *Spartina patens* was common in both xeric and hydric environments. *D. spicata* is apparently at a competitive advantage over *S. patens* in hypersaline conditions, but is otherwise competitively inferior (Bertness and Ellison 1987, Bertness 1991a, Costa et al. 2003). The xerophytic and hydrophytic pairs differed most in their association with nutrients such as boron (Fig. 50) and magnesium (Fig. 52) and in affinity for fresh water (Fig. 56). *Spartina patens*, which has been shown to have a low tolerance for chronic inundation, was nevertheless either similar in environmental factor affinity to hydrophytes or intermediate (Bertness 1991b).

Both *Hydrocotyle verticellata* and *Centella erecta* are members of the carrot family, Apiaceae; stoloniferous, low-growing herbs; similar in appearance; and reputed to be hydrophytic (Radford et al. 1968). Nevertheless, I observed in the field that they did not occur near each other. Regardless of being hydrophytes, both species were different with regard to most environmental factors (Fig. 50, e.g.; Fig. 56).

*Aralia spinosa* is a small (< 4 m) tree in the ivy family, Araliaceae, which is considered allied to or part of the Apiaceae. I only found it growing in the same area as *Centella erecta*. For most factors, it was either similar in affinity to *C. erecta* or intermediate between *C. erecta* and *Hydrocotyle verticellata*. A notable exception was the high soil ammonium found with *A. spinosa* (Fig. 55).

I compared the grass *Festuca rubra* and the tree *Juniperus virginiana* based on my *a priori* observations that 1) they both seemed to have an affinity for each other and

2) *F. rubra* was nearly always found in the margin of the shrub – summit interface. Both species were similar in affinity to most factors.

TABLE 15. Pearson's  $r$  correlation coefficients between environmental factors and three axes of a canonical correspondence analysis ordination of dune and pimple species.

Axis 1: 11 %		Axis 2: 9 %		Axis 3: 6 %	
	$r$		$r$		$r$
B	-0.871	Fe	-0.736	OM	-0.305
Zn	-0.842	MgSat	-0.542	NH <sub>4</sub>	0.2
Mg	-0.82	OM	-0.523	Mg	-0.19
Fe	-0.737	CaSat	0.279	Ca	-0.177
CEC	-0.701	Mg	-0.275	CEC	-0.174
Ca	-0.634	Mn	0.276	Mn	-0.155
P	-0.633	CEC	-0.203	Zn	-0.136
OM	-0.575	Ca	-0.185	P	0.118
MgSat	-0.55	NO <sub>x</sub>	0.18	NO <sub>x</sub>	-0.101
Cu	-0.487	KSat	0.165	water table	0.075
NO <sub>x</sub>	0.417	P	0.159	Fe	-0.059
Mn	0.387	water table	0.125	K	0.056
water table	-0.361	Cu	0.119	B	-0.04
KSat	0.294	Zn	-0.102	CaSat	-0.03
CaSat	0.119	K	0.095	Cu	0.025
K	0.094	B	-0.089	MgSat	0.011
NH <sub>4</sub>	-0.022	NH <sub>4</sub>	-0.06	KSat	0.016

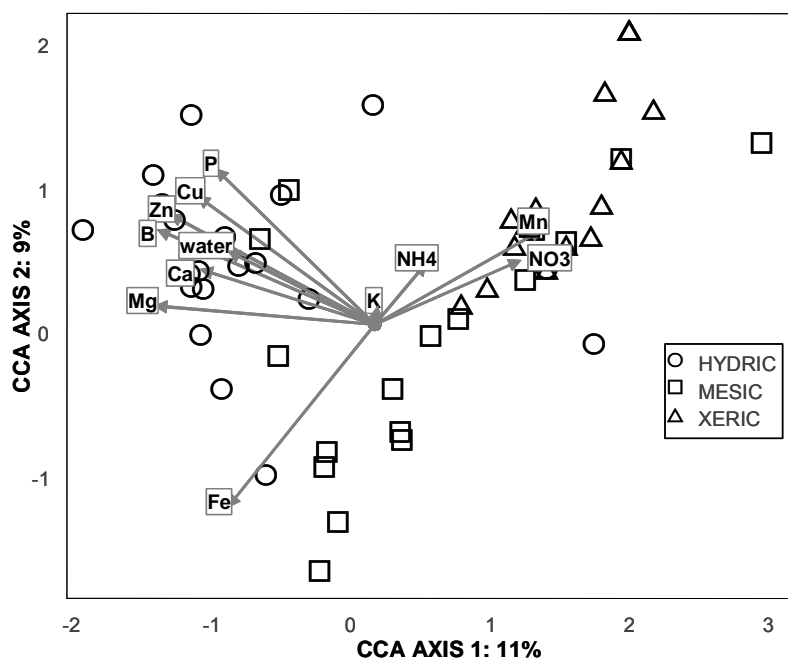


FIG. 49. CCA of main dune and pimple species based on mean environmental variables. In this and subsequent figures, the least important axis was omitted for clarity.

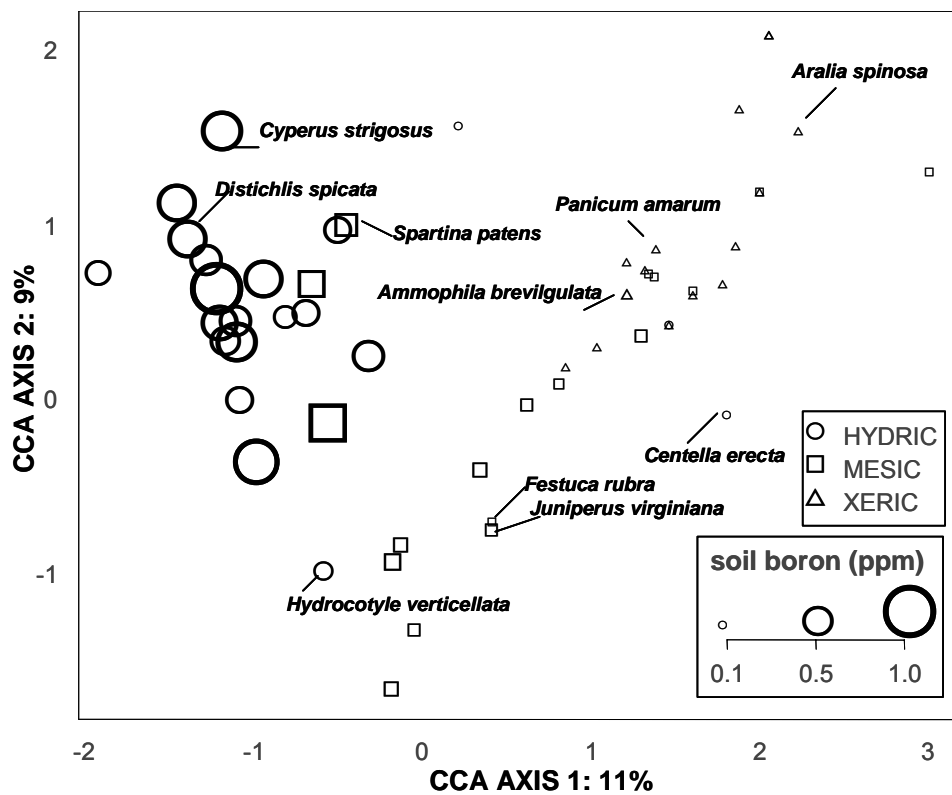


FIG. 50. Overlay of soil boron on a CCA ordination of main dune and pimple species.

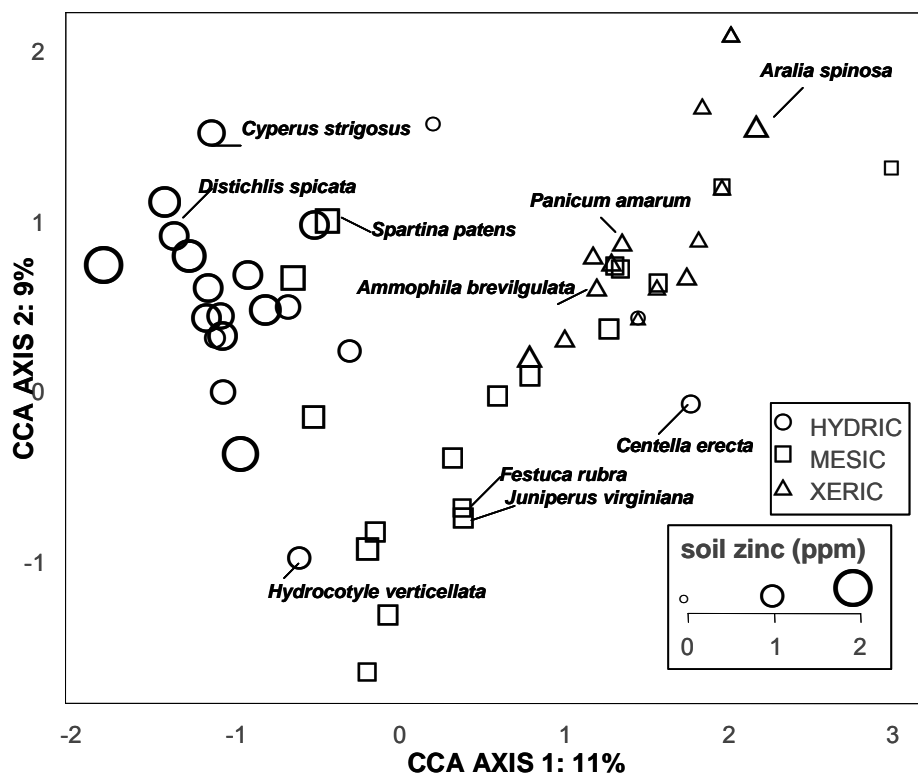


FIG. 51. Overlay of soil zinc on a CCA ordination of dune and pimple species.

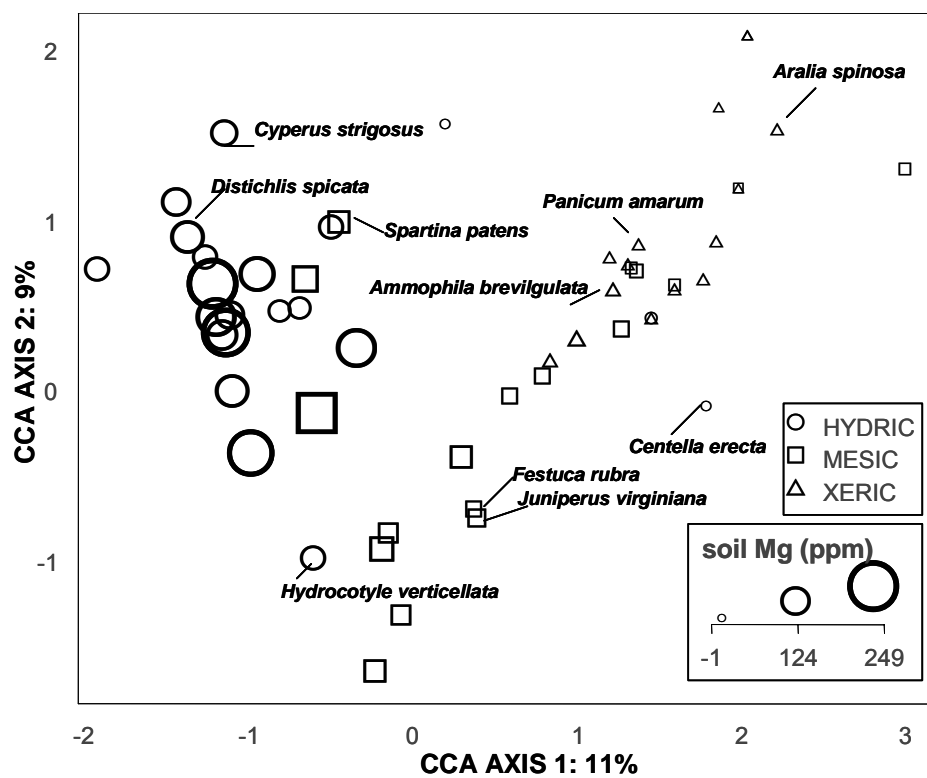


FIG. 52. Overlay of soil magnesium on a CCA ordination of dune and pimple species.

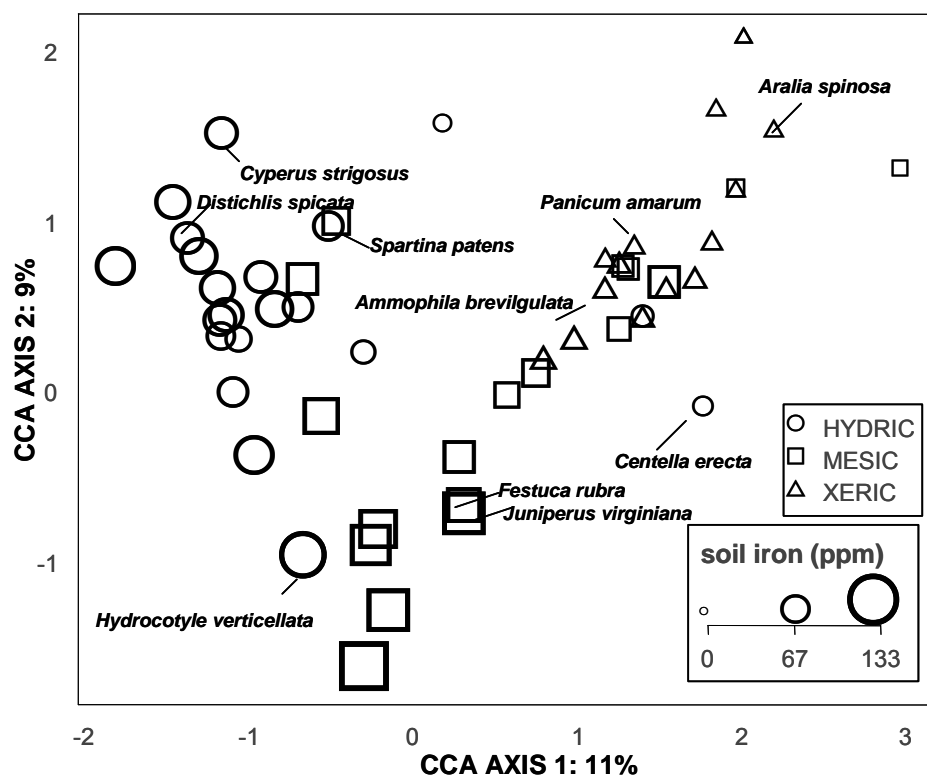


FIG. 53. Overlay of soil iron on a CCA ordination of dune and pimple species.

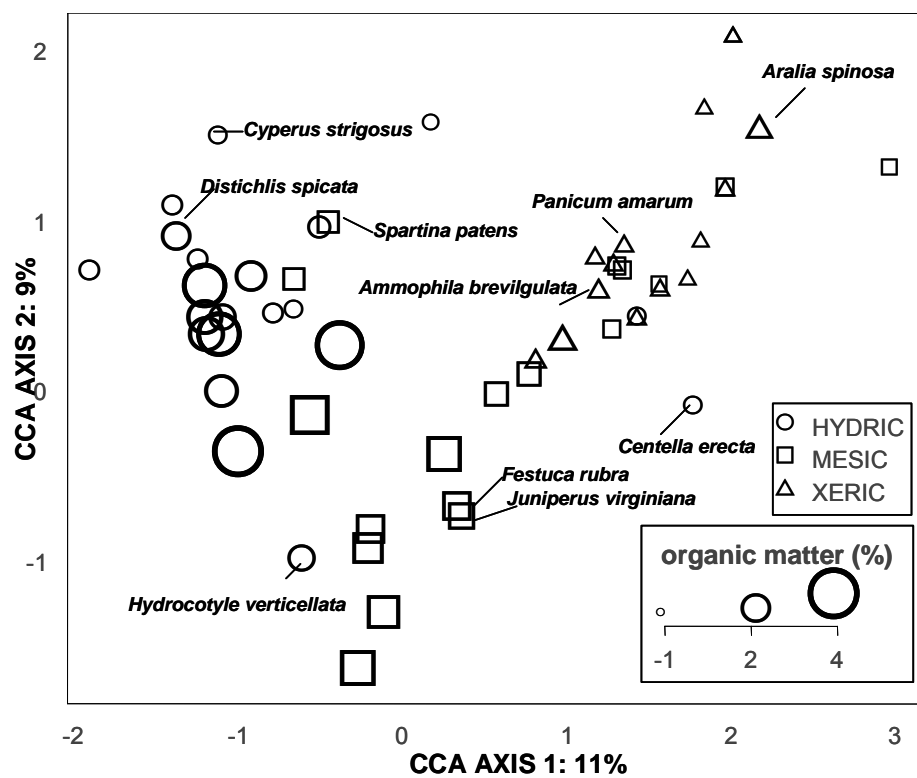


FIG. 54. Overlay of soil organic matter on a CCA ordination of dune and pimple species.

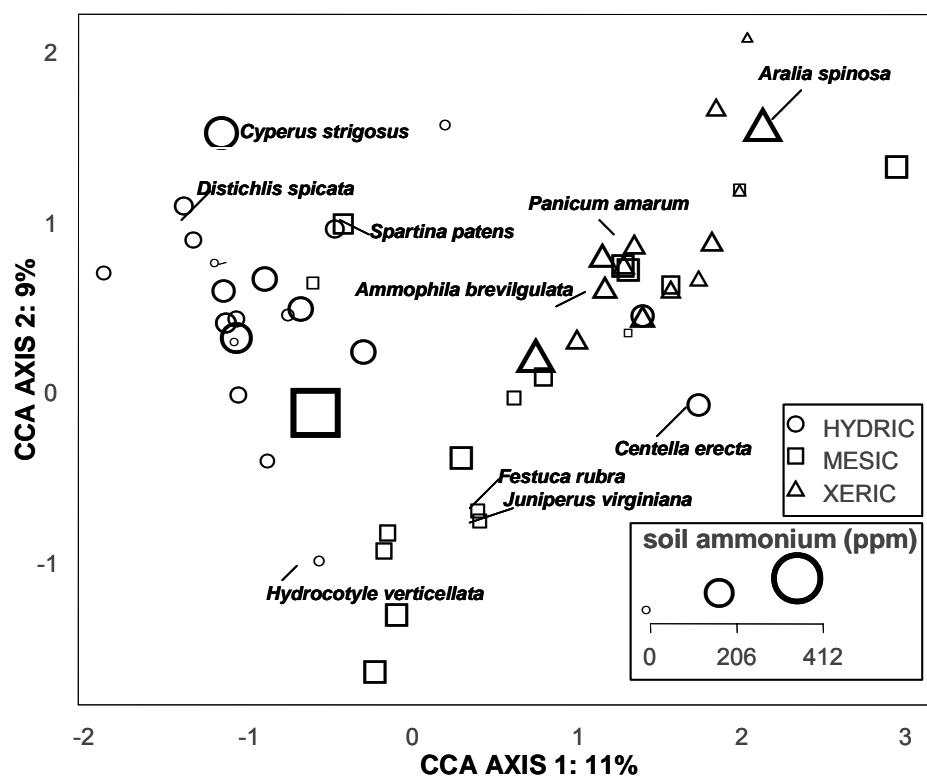


FIG. 55. Overlay of soil ammonium on a CCA ordination of dune and pimple species.



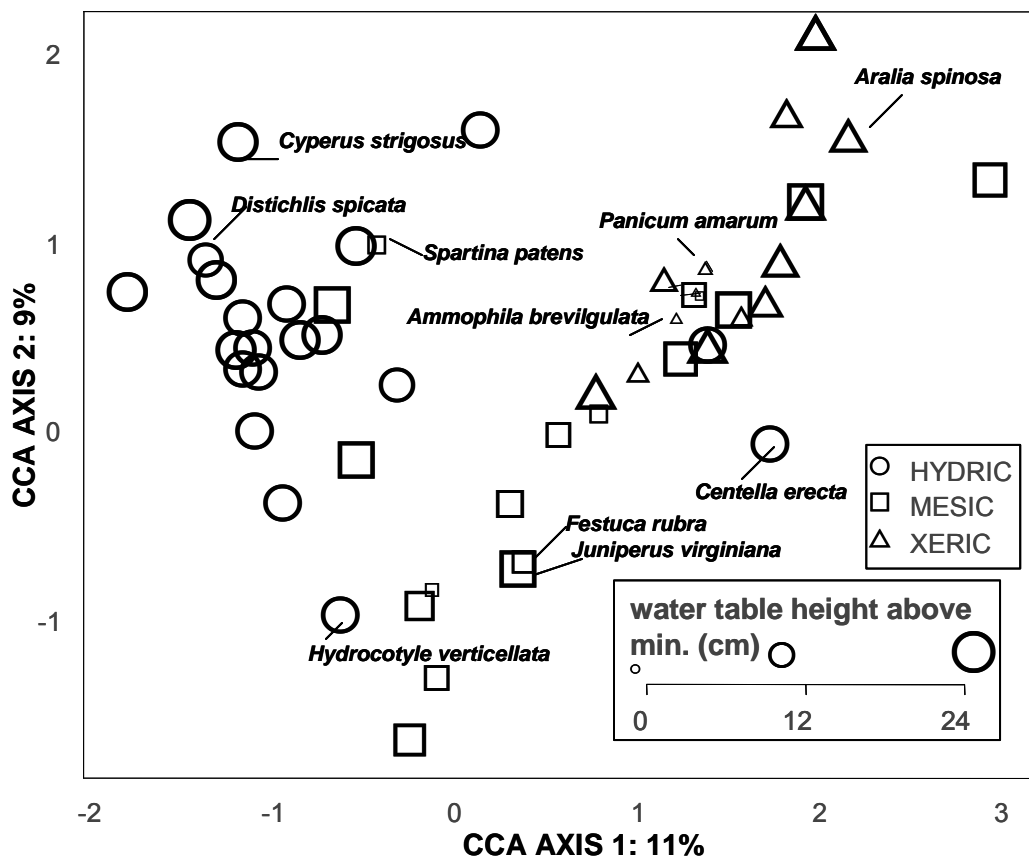


FIG. 56. Overlay of mean position of water table above the average minimum on a CCA ordination of dune and pimple species.

A three-dimensional solution to a non-metric multidimensional scaling ordination of dune and pimple species explained 98 % of variation in the species – environmental factor matrix (Table 16). In contrast to the CCA, species did not form obvious groups based on my *a priori* fresh water-affinity designations (Fig. 57). The two most-correlated factors to each axis were  $\text{NO}_x$  concentration and potassium base saturation (Fig. 57 & Fig. 58); calcium base saturation and iron; and cation-exchange capacity and magnesium (Fig. 59).

TABLE 16. Pearson's  $r$  correlation coefficients between environmental factors and three axes of a non-metric multidimensional scaling ordination of pimple and dune species.

Axis 1: 66 %		Axis 2: 8 %		Axis 3: 24 %	
	$r$		$r$		$r$
NO <sub>x</sub>	-0.826	CaSat	0.365	CEC	0.913
KSat	-0.798	Fe	0.291	Mg	0.878
K	-0.696	NH <sub>4</sub>	0.248	B	0.845
CaSat	0.572	K	0.22	Ca	0.817
Mg	0.565	Mn	0.212	OM	0.761
B	0.557	KSat	0.106	Zn	0.756
Ca	0.547	Zn	0.093	Fe	0.46
MgSat	0.51	P	0.074	P	0.405
Zn	0.481	Cu	0.044	NH <sub>4</sub>	0.252
NH <sub>4</sub>	-0.438	B	0.04	K	0.25
CEC	0.42	MgSat	0.039	water table	0.228
Cu	0.395	CEC	0.035	Cu	0.218
OM	0.395	Mg	0.029	CaSat	-0.168
Fe	0.389	OM	0.02	MgSat	0.088
P	0.351	water table	0.017	KSat	0.068
water table	0.318	NO <sub>x</sub>	0.004	Mn	-0.014
Mn	-0.248	Ca	0.001	NO <sub>x</sub>	-0.017

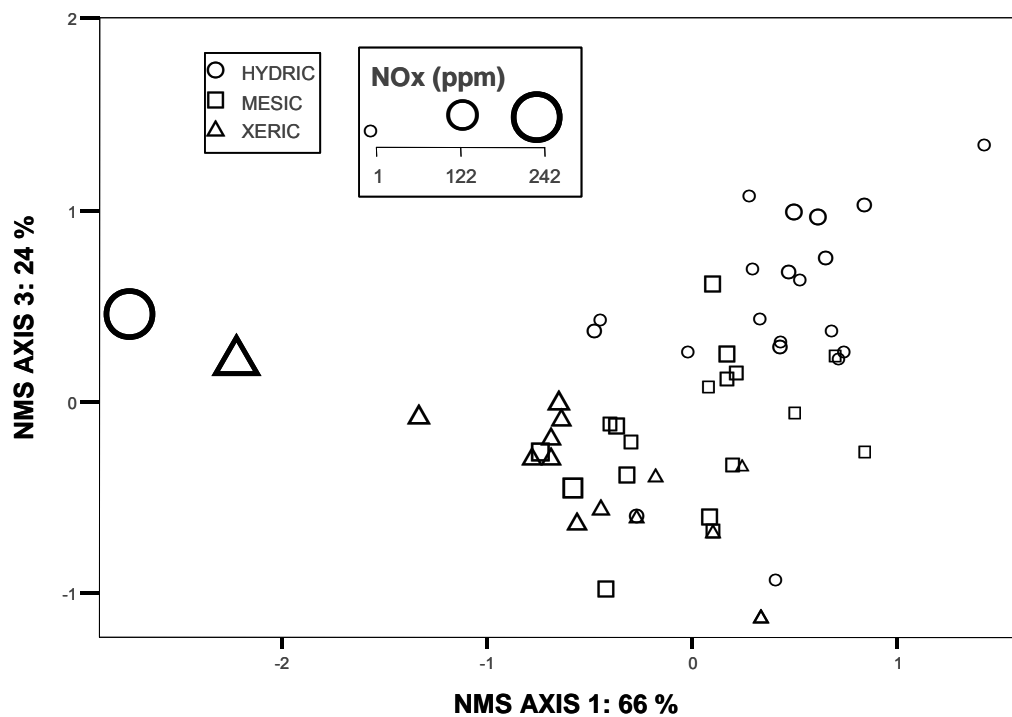


FIG. 57. Overlay of NO<sub>x</sub> concentration on pimple and dune species in NMS ordination.

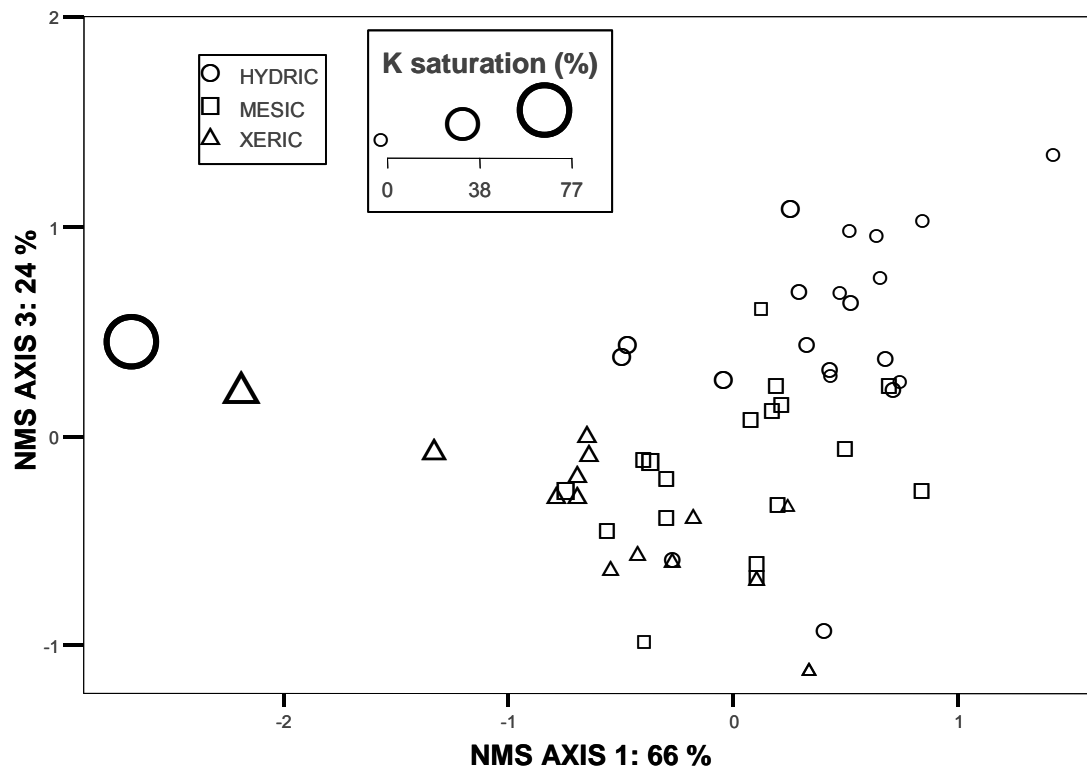


FIG. 58. Overlay of potassium base saturation on pimple and dune species in an NMS ordination.

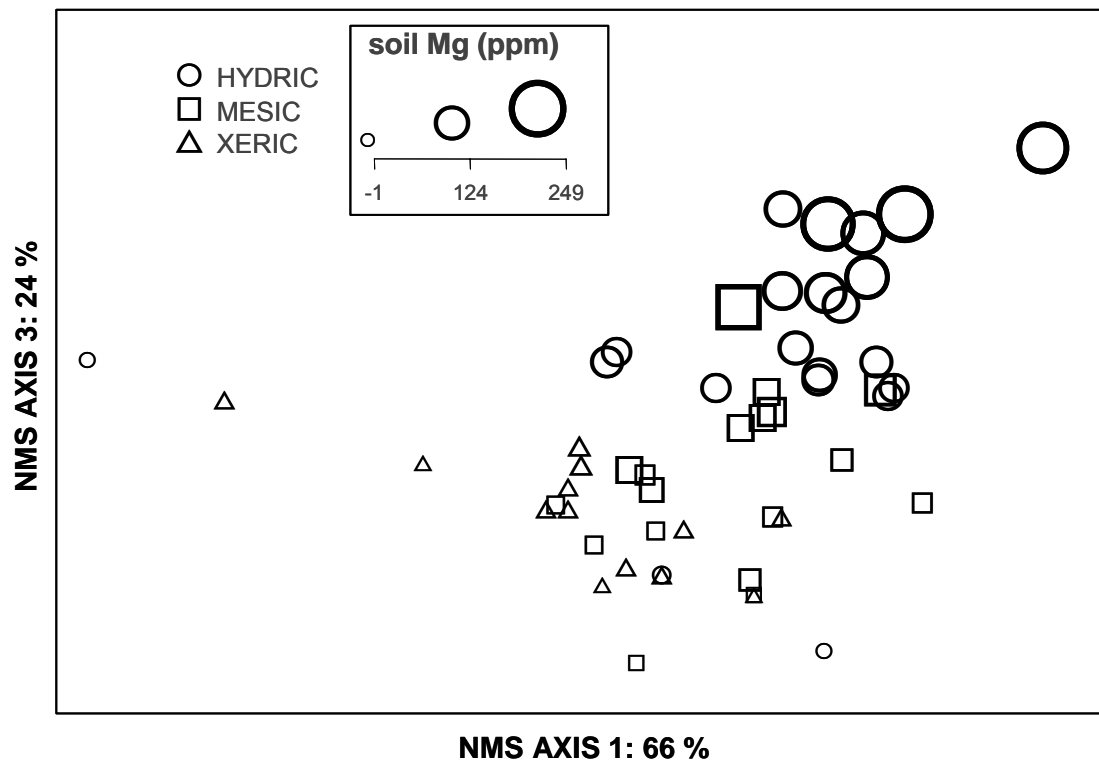


FIG. 59. Overlay of magnesium concentration on dune and pimple species in an NMS ordination.

*Summary.* As with the ordinations of pimple and dune transects, boron, magnesium, calcium, and cation-exchange capacity explained the most variation among dune and pimple species. Also similar to the transect ordinations is the difference in the importance of potassium between NMS and CCA. Water table was less important to species ordinations than to transect ordinations, and organic matter content was of greater importance in species ordinations.

*Species ordinations: pimple species and all recorded factors*

Canonical correspondence analysis of pimple species abundances in transects versus mean environmental variables for each species explained 32 % of variation with the first three axes (Fig. 60; Table 17). Some of the same variables that were important in explaining species distributions in the combined pimple – main dune data were still important, e.g., potassium, ammonium, and iron (Fig. 61 – Fig. 63). Water table position was more important in pimple only CCA, and boron was much less important.

A two-dimensional non-metric multidimensional scaling ordination of pimple species explained 93 % of variation in the data (Table 18; Fig. 64). Potassium concentration and base saturation were most correlated to the first axis (Fig. 65), and ammonium concentration and cation-exchange capacity were most important to the second (Fig. 66). Fresh water availability was of intermediate importance.

*Summary.* Most of the same factors that were important to describing variation among pimple transects were also important to explaining variation among pimple species, with some exceptions. Potassium, of intermediate importance to explaining pimple transects, was the most important factor for describing variation among pimple species. Although among the factors describing the most variation, water table and

elevation were not as important in ordinations of species as they were in ordinations of transects.

I weighted the Pearson's  $r$  correlation coefficients of the factors by the explanatory value of the axes in all the ordinations. Potassium, cation-exchange capacity, water table position, calcium, magnesium and boron were most important in explaining variation in the data. Phosphorus, nitrogen (especially as  $\text{NH}_4$ ), manganese, copper, slope, and aspect were the least important.

TABLE 17. Pearson's  $r$  correlation coefficients between environmental factors and three axes of a canonical correspondence analysis ordination of pimple species.

Axis 1: 12 %		Axis 2: 11 %		Axis 3: 9 %	
	$r$		$r$		$r$
K	0.567	$\text{NH}_4$	0.536	Fe	-0.38
KSat	0.552	O horizon	0.522	OM	-0.345
MgSat	-0.536	water table	0.451	Mn	-0.305
O horizon	0.486	Elevation	-0.447	slope	0.268
CEC	0.432	Mn	-0.379	$\text{NO}_x$	0.237
Fe	-0.387	Slope	0.326	Zn	-0.214
Slope	0.381	Zn	0.246	elevation	0.212
$\text{NH}_4$	0.368	MgSat	0.242	CaSat	-0.183
Zn	-0.366	K	-0.229	Ca	-0.18
OM	-0.348	KSat	-0.225	B	-0.176
Ca	0.256	Fe	0.211	salinity	-0.17
Mn	0.252	B	0.182	O horizon	-0.158
Cu	-0.211	East	-0.167	water table	-0.148
East	0.184	North	0.136	K	0.125
$\text{NO}_x$	-0.181	Mg	0.087	KSat	0.123
Mg	0.18	$\text{NO}_x$	-0.08	north	-0.105
Salinity	-0.095	Ca	0.074	Mg	-0.088
water table	0.088	Cu	0.058	$\text{NH}_4$	0.076
Elevation	-0.082	CEC	-0.039	MgSat	0.064
B	0.082	Salinity	0.048	east	-0.061
North	-0.047	P	0.05	CEC	-0.051
P	0.031	OM	0.036	Cu	-0.045
CaSat	-0.01	CaSat	-0.017	P	-0.021

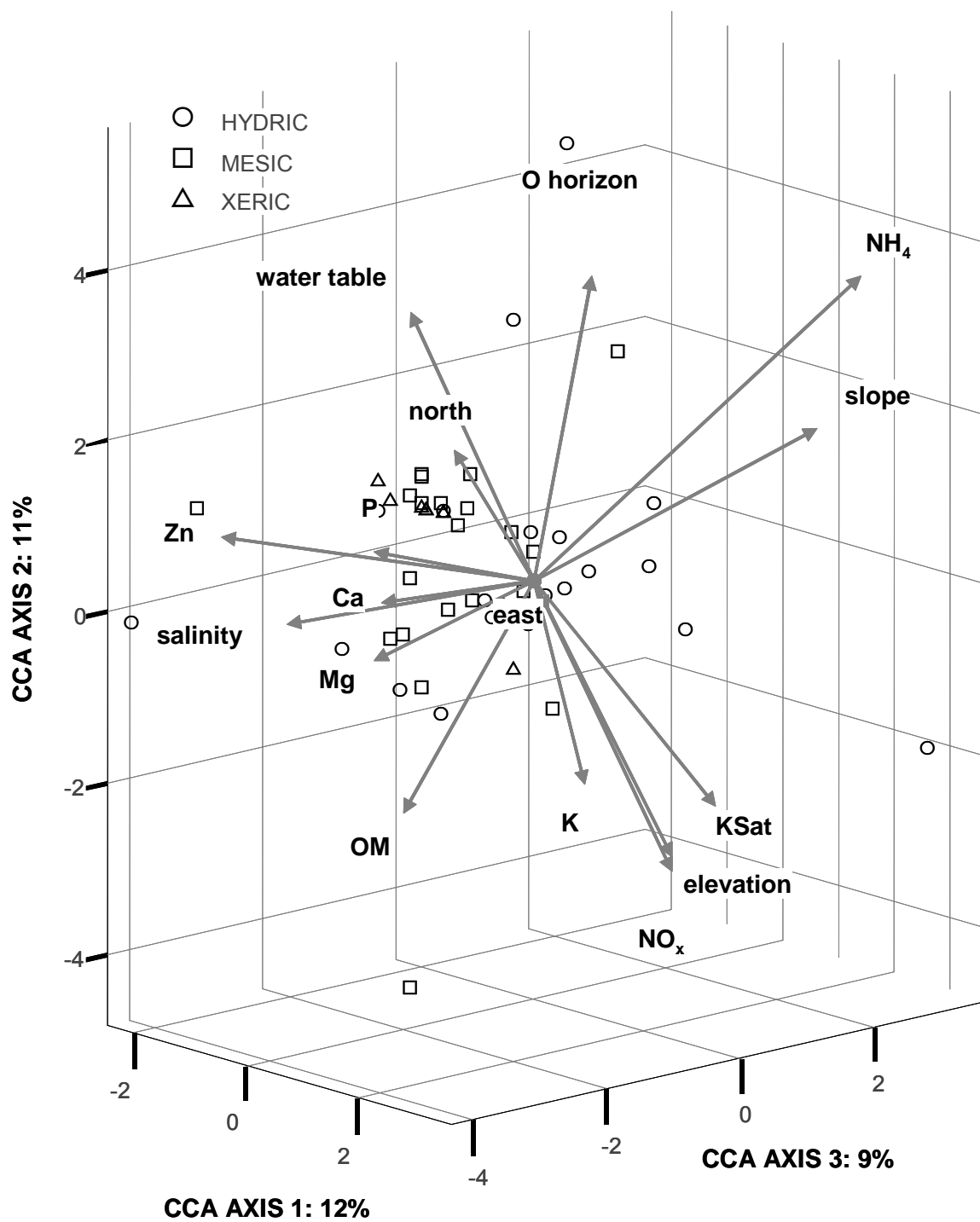


FIG. 60. Canonical correspondence analysis of pimple species based on environmental factors.

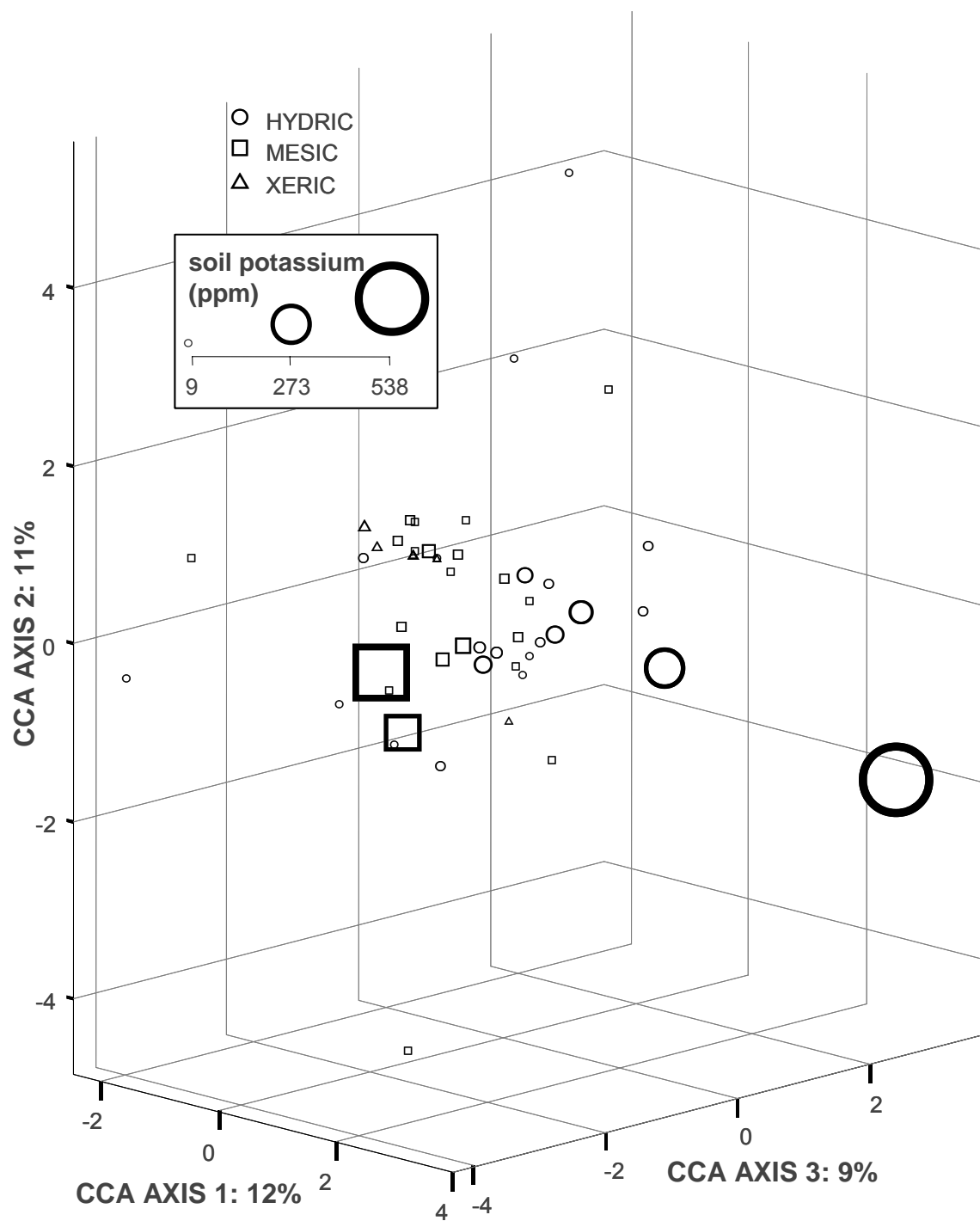


FIG. 61. Overlay of mean soil potassium on pimple species in a CCA ordination.

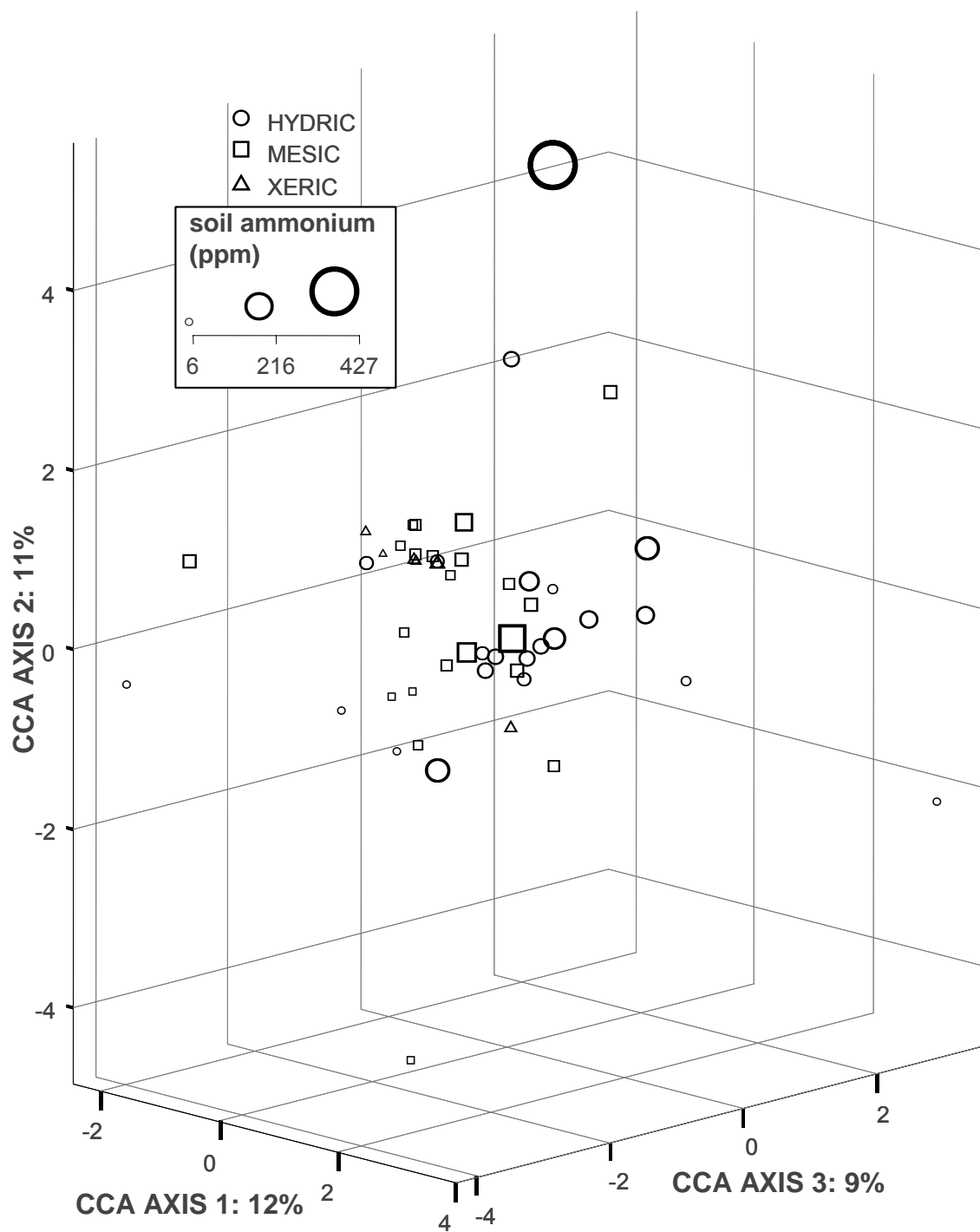


FIG. 62. Overlay of soil ammonium on mire species in a CCA ordination.



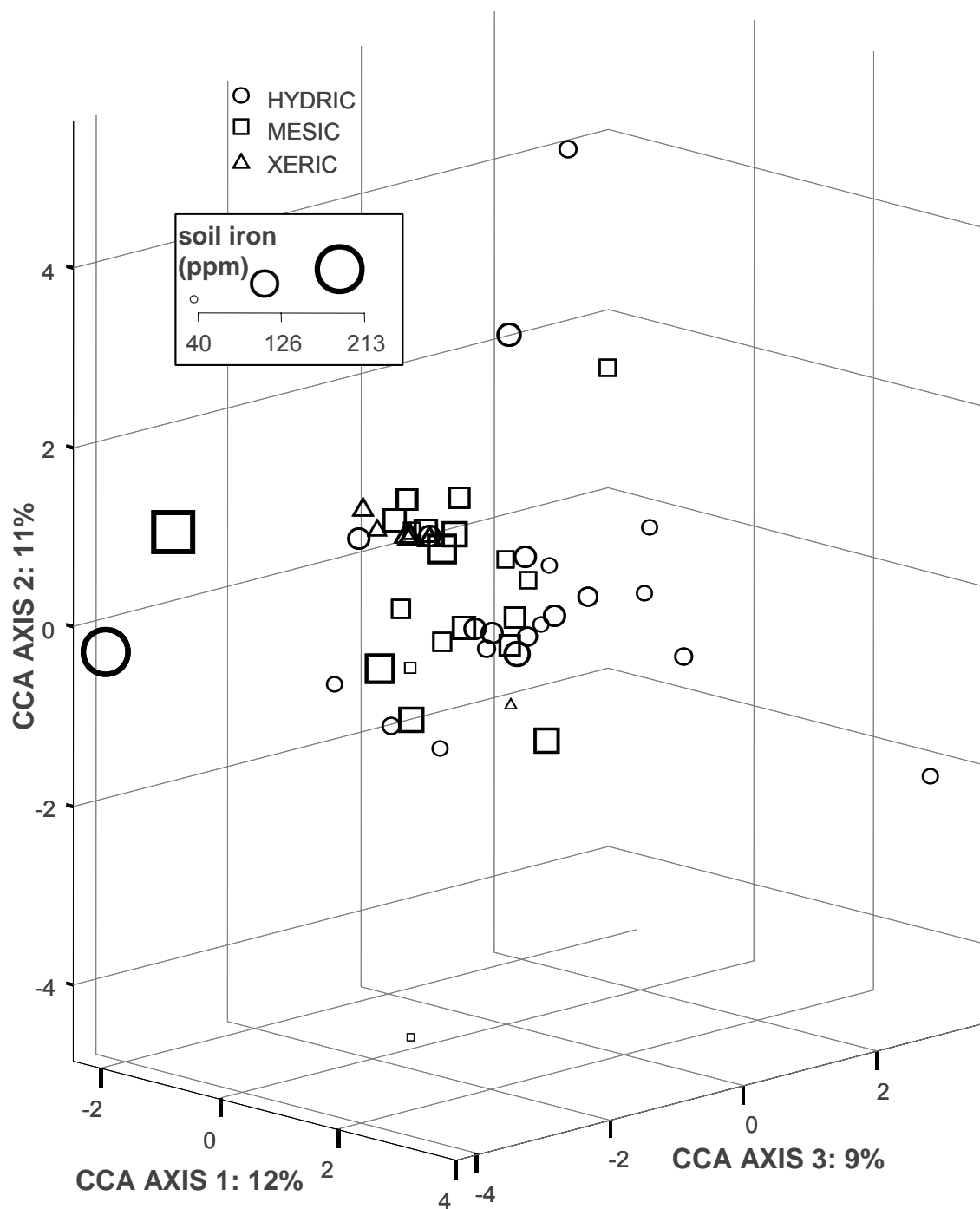


FIG. 63. Overlay of mean soil iron concentrations on pimple species in a CCA ordination.

TABLE 18. Pearson's  $r$  correlation coefficients between environmental factors and three axes of a non-metric multidimensional scaling ordination of pimple species.

Axis 1: 65 %		Axis 2: 28 %	
	$r$		$r$
K	-0.846	NH <sub>4</sub>	-0.673
KSat	-0.81	CEC	0.669
CEC	-0.661	Ca	0.587
MgSat	0.655	Mg	0.574
O horizon	-0.577	B	0.555
Fe	0.457	P	0.513
Ca	-0.419	Zn	0.509
B	-0.406	Cu	0.462
water table	-0.38	K	0.459
elevation	0.378	MgSat	-0.429
OM	0.359	NO <sub>x</sub>	-0.428
Mg	-0.345	KSat	0.422
NH <sub>4</sub>	-0.319	slope	-0.387
slope	-0.267	water table	0.33
P	-0.24	elevation	-0.303
NO <sub>x</sub>	0.184	east	0.198
Mn	-0.168	north	-0.115
Cu	-0.112	O horizon	-0.098
CaSat	0.078	Mn	0.078
east	-0.03	OM	-0.064
north	-0.03	CaSat	0.055
Zn	0.035	Fe	-0.041

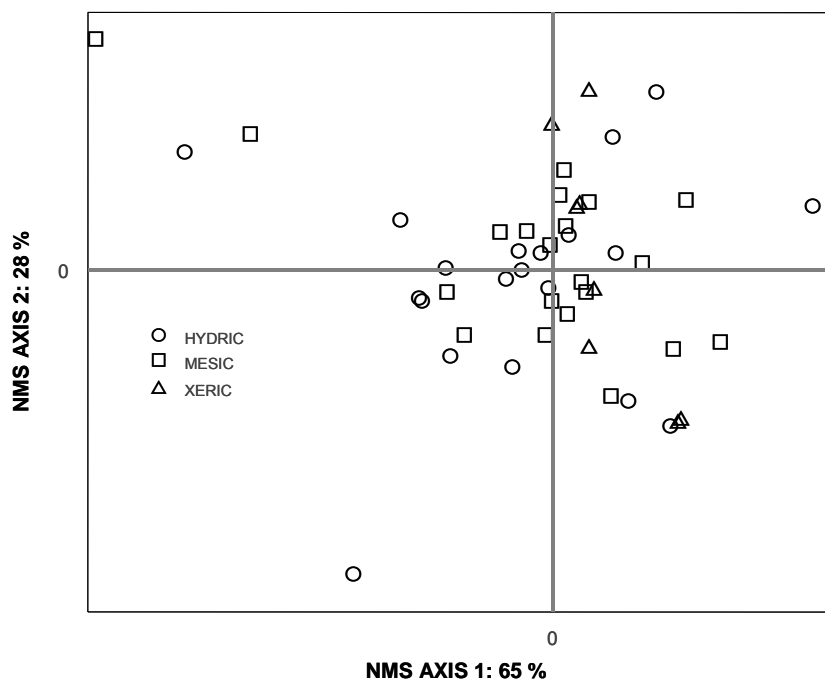


FIG. 64. Two-axis non-metric multidimensional scaling ordination of pimple species based on environmental variables.

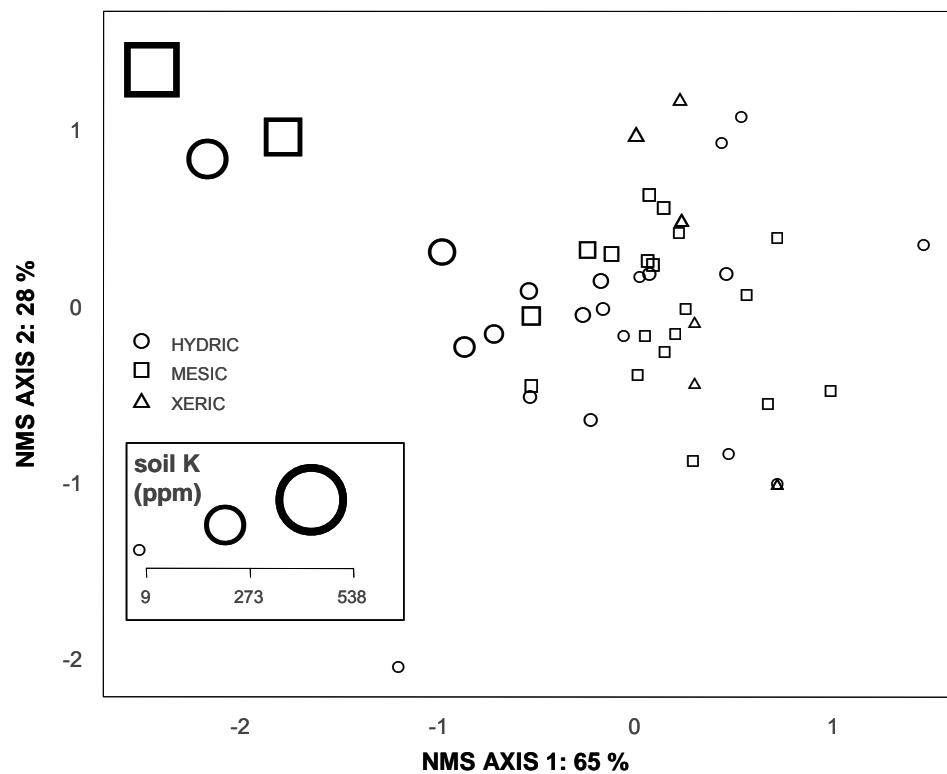


FIG. 65. Overlay of potassium concentration on pimples in an NMS ordination.

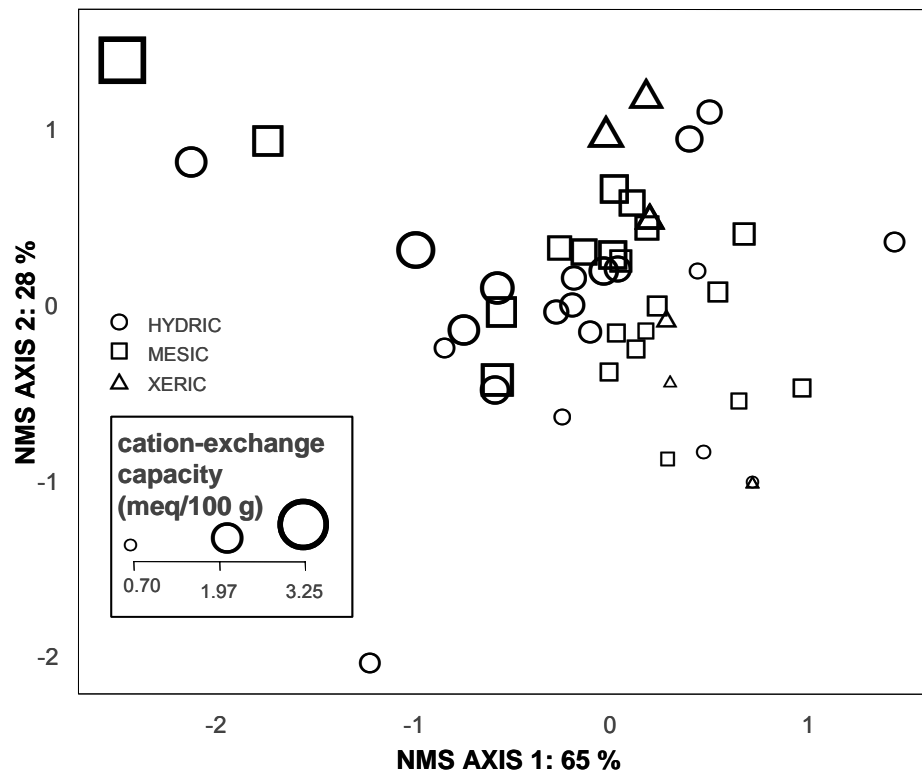


FIG. 66. Overlay of cation-exchange capacity on pimples in an NMS ordination.

## DISCUSSION

*Transect ordinations*

*Pimple and main dune transects.* A surprising result of the ordinations of pimple and reference transects is that water table position was often of secondary importance, considering the hypothesized importance of that 'free surface'. Perhaps this is because there were a disproportionate number of xeric reference plots.

Other factors that were highly correlated with ordination axes, however, may reflect the influence of water. Because the routinely flooded plots had gleyed soils and smelled of sulfides, I assumed they were anoxic and reducing environments and predicted that ammonium should be the most common inorganic nitrogen source there (Pearsall 1938, Brown et al. 1990, Chambers et al. 1992, Tobias et al. 2001, Brady and Weil 2002). Indeed, marsh, shrub, and summit transects did sort themselves along axes highly correlated with ammonium concentrations.

A likely source of many of the mineral and metal micronutrients is deposition from the atmosphere rather than the ocean, either as particulates or in precipitation. Some elements such as boron and potassium are often found in high concentrations in coastal landscapes because they are both deposited from salt spray. Pimples are on the interior of the island and sheltered from spray, except in major storms, and it seems likely that the presence of some elements in and around pimples is a historical artifact of such events. Many mineral nutrients are easily leached and would likely be less abundant in more well-drained soils (Boyce 1954, Willis and Yemm 1961, Brooks and DeWall 1976, Westman 1983, Bricker 1993, Bardgett et al. 2001).

Inspection of ordination axes to which water has a correlation coefficient greater than 0.5 (absolute value) reveals that most mineral nutrients are correlated to axes in the same direction (and often to a similar extent) as water table position. This suggests that mineral nutrients are being leached from drier microhabitats but are less labile in wet areas (Bricker 1993, Khedr and Lovett-Doust 2000, Bardgett et al. 2001, Shumway and Banks 2001).  $\text{NO}_x$  concentrations were usually negatively associated with water; this could be due to inputs from *M. cerifera* nitrogen fixers and litter (Vitousek and Howarth 1991, Semones 1994, Wijnholds and Young 2000, Shumway and Banks 2001). Furthermore, there may be even more indirect relationships to water availability among other environmental factors. For example, calcium often complexes with soil organic matter, and organic matter is typically highest in wet soils whose anoxic conditions reduce decomposition rates (Khedr and Lovett-Doust 2000, Brady and Weil 2002). Organic matter in the mineral horizon and organic horizon thickness, nevertheless, were relatively unimportant to explaining diversity in most ordinations. This is surprising considering that, (1) after soil moisture, soil organic content was an easily observable factor differentiating microhabitat types in the field and (2) organic matter is important for water and nutrient retention in sandy soils (Brady and Weil 2002).

Phosphorus, iron, manganese, and copper had conspicuously low contributions to explaining differences among transects. The latter three are generally deposited on coastal dunes in sufficient amounts for plant growth by sea water and salt spray, but pimples and interior dunes are probably too far inland to receive much spray and have a low overwash frequency (Boyce 1954, Bricker 1993, Hayden et al. 1995). Salt spray is usually the sole source of phosphorus in coastal dunes, and it is typically not supplied in

amounts optimal for plant growth (Boyce 1954). Whether or not these nutrients are limited, they appear to be distributed too uniformly or too haphazardly to be of use in delineating similar groupings of transects.

In all ordinations, reference transects formed groupings that were distinct from pimple transects. The difference in environmental conditions between pimples and main dunes could be inferred as a very important driver of the differences in assemblage composition described in the previous chapter.

*Pimple transects.* The extra physiographic factors available in pimple transect data along with salinity surpass nutrient concentrations as important descriptors of variation between transects. It is not surprising that elevation and water table position are important descriptors of variation among pimple transects because transects were chosen and stratified based on elevation and water presence. The importance of salinity in ordinating transects was surprising because, although pimples were on a coastal barrier island, they are in a freshwater ecosystem. Most coastal dunes, moreover, have low salinities (Boyce 1954), and it would be reasonable to assume that salinity would not vary much among pimples.

It is noteworthy, nevertheless, that many of the same nutrients important in the ordination of dune and pimple transects together were also important to ordination axes for pimple transects alone. Differences in nutrients like boron, magnesium, and calcium varied enough between pimple transects to be useful discriminators in ordinations of them.

### *Species ordinations*

The purpose for ordination of transects based on environmental factors was simply to describe how transects varied. The one caveat to be made in interpreting ordinations of species based on environmental factors is that it is difficult to determine whether relationships are due to coincidence or causation (ter Braak and Barendregt 1985, ter Braak 1986). It is likely that in cases where a factor is less or more important to species ordinations than to transect ordinations, a relationship between that factor and species distributions is not just spatial and coincidental. The coincidental spatial distributions of species and environmental conditions do not necessarily indicate a causative mechanism (Bray and Curtis 1957, Gauch 1973, Gauch et al. 1977, Gauch 1982b, Minchin 1987, Clarke 1993, Økland 1996, Trejo-Torres and Ackerman 2002, Palmer 2007). Nutrients that explained the most variation may co-occur with a particular kind of species because of other environmental conditions and could give some species competitive advantages.

*Pimple and dune species.* Depending on the test used, my *a priori* evaluations of species' affinity to water predicted groupings fairly well. That notwithstanding, it is noteworthy that explanatory contribution to ordinations of nutrients like boron, magnesium, and calcium and cation-exchange capacity were generally higher than water table position, even more so than in transect ordinations.

Boron was a major predictor of species presence in most ordinations, and tended to be associated with hydrophytes. As stated previously, high boron concentration is found in soils influenced by ocean water (Boyce 1954, Boon and MacIntyre 1968, Brooks and DeWall 1976, Rozema et al. 1992). Boron may be more plentiful in wet areas

of the island directly through sea water upwelling and storm water overwash and indirectly as it is leached from dunes into ground water (Boon and MacIntyre 1968, Brooks and DeWall 1976, Bardgett et al. 2001). While higher concentrations of boron in the marsh is coincidental, it probably also determines species distributions. Although an essential micronutrient, boron is toxic to most plants in amounts only ten times that of optimal fertilizing concentrations (Rozema et al. 1992). Rozema et al. (1992) demonstrated that six graminoid and forb halophyte species (including a species of *Spartina*) were generally more tolerant of high levels of boron than glycophytes, probably as an adaptation to the high concentration of boron in sea water. Although swales between dunes on Hog Island are essentially freshwater marshes, many of the dominant hydrophytes are salt tolerant or even facultatively halophytic, e.g. *Spartina patens* and *Distichlis spicata*, as are some uncommon species, e.g. *Typha angustifolia* (Kearney 1904, Boyce 1954, Radford et al. 1968, Shumway 1995). Species that can survive both inundated and saline conditions, i.e. halophytic hydrophytes or vice versa, may be at the greatest competitive advantage for life in the swale marshes of Hog Island.

Magnesium and calcium are readily supplied to dune ecosystems by salt spray, but leaching and plant uptake may still make them limiting depending on history and location of the dune (Kearney 1904, Olsson-Seffer 1909, Boyce 1954, Gorham 1958, Willis and Yemm 1961, Willis 1963, Pemadasa and Lovell 1974, Hester and Mendelssohn 1990, Bardgett et al. 2001, Shumway and Banks 2001). Older dunes that are removed from the influence of salt spray and inundation, as in the pimple and main dunes of this study, have been found to have much lower concentrations of both cations (Boyce 1954, Willis and Yemm 1961). Differences in availability of magnesium and



calcium have been implicated in dominance shifts and growth responses in some of the same species and ones similar to them (Clayton 1972, van der Valk 1974, Hester and Mendelssohn 1990, Khedr and Lovett-Doust 2000). For example, fertilization of dunes with macronutrients (N, P, K) and micronutrients (Ca and Mg ; if severely limited) elicited a shift in dominance from a beach-colonizing grass (*Ammophila* sp.) to a generalist grass with higher nutrient requirements (*Festuca rubra*) (Gorham 1958, Willis 1963). Magnesium and calcium-related alkalinity is important to growth of endangered basiphilous swale species in the Netherlands; one of those species, *Samolus valerandi*, is also an uncommon member of the Hog Island marsh flora (Bekker et al. 1999, Lammerts et al. 1999, Lammerts et al. 2001).

In these results, importance of calcium and magnesium increases along the continuum from xerophytic to hydrophytic species. This suggests a more or less coincidental association between calcium, magnesium, and species growing in particular zones: 1) Xeric summits should have the lowest amounts of the two cations since losses from leaching outpace the inputs from precipitation or occasional storm-driven salt spray in these sheltered areas; 2) hydric marshes receive the leachates; and 3) shrub zones may retain intermediate levels of cations in the thick organic layer (Kearney 1904, Olsson-Seffer 1909, Evans 1953, Boyce 1954, Clayton 1972, van der Valk 1974, Gorham et al. 1979, Shumway and Banks 2001, Brady and Weil 2002).

Magnesium and calcium are most likely to be important to species distribution where they are most limited, in xeric summits. For example, the grass *Ammophila breviligulata*, which is a dominant species on mainline dune summits, is rarely found on pimple summits, whereas *Festuca rubra* is relatively more abundant on pimples than

main dunes (pers. obs.). This could be a situation similar to the one already described (Willis 1963): In pimple summits (vs. main dune summits) there is an enhanced edge influence of the shrub zone and its higher nutrient retention in the organic layer. Indeed, *F. rubra* occurs nearly exclusively along the shrub edges in the main dunes (pers. obs.; F. Day, unpublished data).

Concentrations of magnesium, calcium, and boron are correlated with each other and with water table position (although this is a weaker correlation). There is therefore the possibility that these minerals have no direct effect on plant distributions and are simply indicating the importance of water alone. Based on the importance of these nutrients to plant health, however, I assert that the importance of boron, calcium and magnesium to assemblage composition explains some of the importance of water .

Zinc was of intermediate importance in explaining species distributions. This is due partly to the aforementioned syndrome of high marsh – low summit concentrations due to leaching. Zinc has been known to interfere with phosphorus utilization in plants and may therefore have a causative role to play in species distributions (Hester and Mendelssohn 1990, Bricker 1993).

The nutrients that would seem most likely to influence species distributions were not indicated as such by the analyses. Nitrogen and phosphorus are the major limiting nutrients in dune ecosystems (Willis and Yemm 1961, Willis 1963, Keefe and Boynton 1973, Pemadasa and Lovell 1974, Gorham et al. 1979, Westman 1983, Hester and Mendelssohn 1990, Vitousek and Howarth 1991, Bardgett et al. 2001, Pausas and Austin 2001, Shumway and Banks 2001). It was noteworthy that 1) some xeric species (e.g., *Ammophila breviligulata*, and especially *Aralia spinosa*) were associated with higher

ammonium levels than most xerophytes and 2) ammonium concentration varied considerable among hydrophytes (e.g., *Centella erecta* and *Hydrocotyle verticellata*; Fig. 55). Since ammonium levels should be highest in wet soils, I expected to see species affinities for ammonium follow a water-affinity gradient, similar to boron (Fig. 50). Although it is likely that ability to use ammonium varies among the species sampled, there could be other reasons for the association that may or may not be causative. For example I frequently noticed rabbit droppings in the dune with *A. spinosa* and *C. erecta*, and this could have produced higher than normal ammonium levels for the relatively dry soils there. Whether plants or fertilizer came first cannot be determined conclusively.

Iron, manganese, and copper are essential micronutrients that are usually not limited in coastal systems but become toxic in high amounts or in reduced forms (Jones and Etherington 1971, Jones 1972a, 1972b, Bricker 1993). Perhaps these elements are too sparsely distributed to have an appreciable effect.

*Pimple species.* The only major differences between factors determined to be important in pimple and main dune species ordinations and ordinations of species only is the increased importance of water availability (water table position + elevation), cation-exchange capacity, and potassium availability. The importance of water to species distribution is self-evident. The importance of elevation, not only to water availability, but also in terms of exposure, organic matter accumulation, etc. is similarly easy to see (Olsson-Seffer 1909).

Since the soil on the dunes is a uniform, well-sorted sand, cation-exchange capacity probably represents the contributions of the organic layer and organic matter content to nutrient retention (Lammerts et al. 1999, Brady and Weil 2002). This is

probably why CEC was more important to the ordinations than either organic matter content or O-horizon.

Of the three plant macronutrients, potassium is least likely to be limited in a coastal system. As with other nutrients, its importance to hydric and mesic species is partially coincidental due to leaching and organic layer retention (Gorham 1958, Willis 1963, Jones 1975a). It could have a potential role to play in iron or manganese toxicity in the marshes (Jones 1972a, 1972b, 1975a). It has been shown to influence growth in some dune species, especially when input is limited by lack of salt spray (Boyce 1954, Gorham 1958, 1961, Willis and Yemm 1961, Willis 1963, Clayton 1972, Hester and Mendelsohn 1990).

The other physiographic factors added to the pimple species data set, slope and aspect (divided here into eastern and northern exposure), are proxies for other factors such as wind exposure and insolation, and have been long known to influence plant assemblages on dunes (Olsson-Seffer 1909). The lack of importance of these factors suggests that pimples are too protected from exposure to prevailing winds or salt spray for them to make a difference (Boyce 1954).

One important determinant of plant assemblage structure can not be inferred from this study: interspecific interactions. The importance of competition and facilitation between plants in coastal ecosystems to diversity and species composition is well-established, especially in salt-marshes (Hacker, 1999; Bertness, 1994; Bertness, 1991 ). For example, greater coverage of *Spartina patens* in xeric areas of main dunes vs. pimples may be explained by it being a poorer competitor on pimples. Perhaps some

factor (e.g., shading in the interior of the pimple from *Myrica* litter) gives other species a competitive advantage.

#### CONCLUSIONS

Kruckeberg (1969) wrote that “The edaphic factor — physical and chemical properties of soils — can elicit sharp discontinuities in plants. Sharp discontinuities between soils of highly contrasting lithological origin exert marked selective effects on floras.” Although organic matter, water content, or redox potential may vary in different areas and at different depths, there is effectively only one soil on Hog Island and Parramore Island. There are, however, distinct plant assemblages on and between the dunes, both linear main dune and pimple. Those borders appear to be drawn along edaphic and hydrodynamic lines more than physiographic or historical ones. I assert this because 1) water and nutrient availability were more important to differentiating transects and species than slope or aspect and 2) different-aged main dune plots sorted themselves similarly to each other.

As hypothesized, fresh water availability was an important factor delineating changes in plant assemblages. Only a few species on the island, most notably *Spartina patens*, demonstrate an ability to grow well in both wet and dry areas. Because fresh water is believed to be a driving force behind most of the ecology of the islands, it was surprising to find other factors, e.g. boron, taking such a major role in describing variation. The indirect effect of fresh water on these other factors (e.g. nutrient leaching or nitrogen reduction) cannot be ignored. Overall these findings suggest that nutrient availability as influenced by water is the main cause of shifts in plant assemblage composition, not simply water availability or nutrient availability alone.

## CHAPTER 5

### CONCLUSIONS

#### WATER AND OTHER DRIVERS

My first hypothesis was that fresh water availability was the main driving force behind plant assemblage variation on the barrier islands. My results do indicate that the influence of fresh water on plant assemblages is profound; that was really never in question. Nevertheless, I have found evidence that suggests other factors may be similarly important. Although this is most likely because of those factors' interaction with water, it is noteworthy that the influence of water on plant assemblages is not due simply to differing water requirements of the species involved. I base these conclusions on the implementation of my three research goals.

#### *Goal 1: pimple plant assemblage descriptions*

Plant assemblage composition was markedly different between habitat zones on pimples. It is reasonable to conclude that these differences are because of fresh water, but there were differences within habitat zones that were not readily explainable by water availability. Marsh transects were not uniform combinations of the same hydrophytic graminoids. Rather, the presence of dominant species was patchy and proportions of species varied greatly across the landscape. Summit transects with similar water availability had wide differences in species richness and diversity. Even shrub transects were not all monocultures of *Morella cerifera*. Similar species, such as *Centella* and *Hydrocotyle*, demonstrated apparent differences in habitat preferences, although both were hydrophytic.

*Goal 2: environmental factors*

Transects and species could be grouped by both fresh water availability as well as nutrients, such as boron and potassium. The explanatory value of some of these variables (particularly potassium) could either result from historical events or be driven by outliers. It is impossible to prove that any patterns between species and nutrient distributions are either the result of coincidence or underlying mechanisms. The regularity of the association between some factors (e.g. boron concentration) and species or groups of species suggests that there are some significant causative relationships besides water relations driving changes in assemblage structure.

*Goal 3: comparing main dunes to pimples*

There were differences in diversity measures and assemblage structure between pimple and dune transects. Those differences were most noticeable between main dune and pimple summits. This suggests an influence of fresh water availability since the water table was generally closer to the surface of pimple summits than main dune summits.

Differences between main dune and pimple transects were also explained by other environmental factors besides just water, e.g. boron and cation-exchange capacity. I suggest this is largely due to the influence of *Morella cerifera*. The ratio of shrub thicket perimeter to open summit area is much higher in pimples. For pimple summit assemblages, this could lead to 1) more nutrient input from relatively nitrogen-rich leaf litter, both directly from decomposition, and indirectly through increased nutrient retention; 2) more mesic conditions due to shading; and 3) differences in drainage due to *M. cerifera*'s root system.

### SPATIAL RELATIONSHIPS

My second hypothesis, that pimple size and location would be determinants of diversity had no support from my results. There were other spatial patterns of assemblage structure, however. Besides the obvious differences in diversity and species composition between transects within pimples, there were differences among pimples, between pimples and main dunes, and between Hog Island and Parramore Island Pimples.

### STATISTICS

Although most of my study took place in a roughly  $0.5 \times 1$  km section of a barrier island, describing plant assemblage dynamics there rapidly grew complex. The ordination techniques I used (especially CCA and NMS) were successful in simplifying the patterns of diversity and environmental factors I encountered on the dunes. Although there was still a net of interactions, affinities, and associations, these ordinations helped to untie many of the knots in it. In the search for significant P values, it can be easy to lose sight of the fact that the goal of using statistics in ecology should be to objectively detect and describe real patterns. The techniques I used here were neither new nor particularly rare, but they still are not used as much as they perhaps should, considering their ease of use and interpretation.

### CONCLUSION

Although there may be barrier islands elsewhere in the world with small mounded dunes, pimples as they exist in Virginia's climate and flora are unique. I was first drawn to study them because of their uniqueness and because I wanted to know how assemblages could be packed so tightly into such a small area. I found that fresh water is not the only important ecological factor and that pimple assemblages are not as similar to



main dune assemblages as they may first appear. Although pimples are different from the main dunes, I recommend they be used as experimental units.

At other LTER sites, studying the interactions of abiotic resources and plant species in 'insular' communities has improved understanding and management of imperiled ecosystems. Tundra tree islands in Niwot Ridge are important sinks for soil nutrients; flow of ground water and nutrients between tree islands in the Everglades is a crucial factor in those communities (Holtmeier and Broll 1992, Troxler Gann et al. 2005). Studying the geological and biological processes that make pimples different from the main dunes would be a considerable contribution to the knowledge of the VCR and other coastal barrier ecosystems, especially with respect to succession, species interactions, and dune formation. Such knowledge could also be important for management of narrowly endemic and patchy communities.

Furthermore, continuing research could unravel the question of how pimples form. Past hypotheses were mostly based on geological processes; one proposed biological process, animal excavation, is not likely, based on my experience (Rich 1934, Melton 1935, Dietz 1945, Cross 1964). Two facts indicate that pimple formation is initiated by geological events and completed through biological succession. Their position inside the main dunes, away from the ocean, suggests that they are fragments of foredunes whose development has been arrested by the subsequent formation of another line of dunes. The interaction between the abiotic conditions on pimples and the plants that colonize them are likely responsible for the physiographic and phytosociological differences between pimples and the main dunes. A good course for future work on

pimples would be to examine the role of mycorrhizal associations in their formation and establishment (Koske and Polson 1984, Al-Agely and Reeves 1995).

## APPENDIX

## RESULTS OF ORDINATIONS NOT PRESENT IN MAIN TEXT

TABLE 19. Correlation of environmental factors with the first three axes of a Bray-Curtis ordination of main dunes and pimples (Pearson's r).

Axis 1: 50 %		Axis 2: 15 %		Axis 3: 10 %	
NH <sub>4</sub>	0.59	CEC	0.7	P	0.435
water table	-0.516	Ca	0.679	Fe	-0.348
Zn	-0.364	B	0.616	CaSat	0.326
B	-0.327	Mg	0.614	NH <sub>4</sub>	-0.291
Mg	-0.309	NH <sub>4</sub>	0.56	MgSat	-0.276
NO <sub>x</sub>	0.307	Zn	0.431	Zn	0.269
MgSat	-0.288	MgSat	-0.428	NO <sub>x</sub>	-0.262
Cu	-0.284	Mn	0.413	OM	-0.231
KSat	0.285	NO <sub>x</sub>	0.403	water table	0.218
P	-0.269	K	0.363	Cu	0.207
Ca	-0.253	OM	0.352	Ca	0.122
CEC	-0.243	KSat	0.269	B	0.12
Mn	0.228	P	0.255	KSat	-0.077
Fe	-0.193	Fe	-0.215	CEC	0.06
K	0.099	CaSat	0.154	Mn	0.05
OM	-0.06	Cu	0.15	K	-0.046
CaSat	0.01	water table	0.094	Mg	-0.002

TABLE 20. Pearson's r correlation coefficients for the first three axes of a principal components analysis of main dune and pimple transects versus environmental factors.

Axis 1: 31 %		Axis 2: 19 %		Axis 3: 18 %	
Mg	-0.965	P	0.743	MgSat	-0.92
CEC	-0.952	K	-0.665	Fe	-0.788
Ca	-0.886	KSat	-0.611	Mn	0.677
B	-0.852	Cu	0.597	CaSat	0.668
OM	-0.723	NO <sub>x</sub>	-0.575	water table	-0.561
Zn	-0.655	Zn	0.533	NO <sub>x</sub>	0.265
water table	-0.551	CaSat	0.51	Ca	0.256
NO <sub>x</sub>	-0.512	OM	-0.505	NH <sub>4</sub>	0.237
K	-0.358	water table	0.347	KSat	0.21
NH <sub>4</sub>	-0.347	B	0.321	P	0.163
Cu	-0.289	Fe	-0.18	CEC	0.166
Fe	-0.274	CEC	-0.136	K	0.156
P	-0.213	NH <sub>4</sub>	-0.133	OM	-0.108
Mn	-0.113	Mn	0.078	Cu	-0.037
CaSat	0.055	MgSat	0.05	B	-0.023
MgSat	-0.056	Mg	-0.026	Mg	-0.037
KSat	-0.003	Ca	0.023	Zn	-0.019

TABLE 21. Pearson's r correlation coefficients for three axes of a Bray-Curtis ordination of pimple transects based on environmental factors.

Axis 1: 54 %		Axis 2: 19 %		Axis 3: 8 %	
Salinity	-0.877	water table	-0.577	K	-0.879
water table	-0.577	NO <sub>x</sub>	0.576	KSat	-0.846
Elevation	0.513	elevation	0.556	CEC	-0.554
CaSat	0.443	NH <sub>4</sub>	0.462	MgSat	0.358
MgSat	-0.402	o horizon	-0.455	Fe	0.324
o horizon	-0.383	CEC	-0.439	o horizon	-0.294
Mn	0.38	Cu	-0.384	Mg	-0.277
Fe	-0.376	Zn	-0.351	CaSat	0.276
Mg	-0.319	salinity	-0.349	B	-0.265
CEC	-0.254	Mg	-0.349	Ca	-0.241
Zn	-0.251	K	-0.336	water table	-0.19
B	-0.235	Ca	-0.327	salinity	0.183
K	-0.181	B	-0.289	elevation	0.177
Slope	0.162	slope	0.267	P	-0.129
OM	-0.16	KSat	-0.201	Cu	-0.098
NO <sub>x</sub>	0.137	P	-0.185	NO <sub>x</sub>	0.082
KSat	-0.107	CaSat	0.181	east	0.08
NH <sub>4</sub>	0.101	Mn	0.159	NH <sub>4</sub>	-0.072
Ca	-0.094	east	-0.089	north	0.054
Cu	-0.053	OM	-0.071	Mn	-0.031
North	0.05	MgSat	-0.04	Zn	-0.017
P	-0.044	Fe	-0.041	slope	-0.012

TABLE 22. Pearson's r correlation coefficients for three axes of a principal components analysis ordination of pimple transects based on environmental factors.

Axis 1: 29 %		Axis 2: 18 %		Axis 3: 11 %	
Ca	0.917	CaSat	0.866	KSat	0.897
B	0.912	MgSat	-0.806	K	0.863
CEC	0.85	OM	-0.778	MgSat	0.193
water table	0.82	Fe	-0.771	Fe	0.114
Mg	0.779	Mn	0.547	CEC	0.096
Zn	0.738	salinity	-0.514	CaSat	0.075
Elevation	-0.732	P	0.484	Zn	0.044
P	0.724	Mg	-0.416	salinity	0.042
Cu	0.659	o horizon	-0.399	slope	0.028
o horizon	0.654	water table	-0.337	NO <sub>x</sub>	0.02
NO <sub>x</sub>	-0.428	elevation	0.287	Cu	0.014
Slope	-0.386	K	-0.271	NH <sub>4</sub>	0.013
CaSat	0.227	CEC	-0.249	Mn	0.01
MgSat	-0.22	slope	-0.206	o horizon	0.008
Fe	-0.205	Cu	0.181	water table	0.008
OM	-0.193	KSat	-0.182	elevation	0.005
Salinity	0.178	Zn	0.165	P	0.002
NH <sub>4</sub>	0.176	NH <sub>4</sub>	-0.11	B	0.002
K	0.129	B	-0.103	OM	0.001
Mn	0.106	NO <sub>x</sub>	-0.107	Ca	0.001
North	-0.089	Ca	0.071	north	0.001
East	-0.027	north	0.051	Mg	0

TABLE 23. Pearson's r correlation coefficients between environmental factors and three axes of a Bray-Curtis ordination of pimple and dune species.

Axis 1: 34 %		Axis 2: 40 %		Axis 3: 18 %	
	r		r		r
CEC	0.838	NO <sub>x</sub>	-0.765	Mg	0.562
B	0.829	KSat	-0.751	Ca	0.541
Mg	0.82	K	-0.67	OM	0.502
Zn	0.775	MgSat	0.543	KSat	-0.498
Ca	0.744	Mg	0.529	B	0.495
OM	0.645	B	0.516	CEC	0.473
P	0.495	Ca	0.487	NH <sub>4</sub>	0.442
Fe	0.484	Zn	0.483	K	-0.429
Cu	0.341	CaSat	0.481	NO <sub>x</sub>	-0.383
water table	0.322	Fe	0.445	MgSat	0.361
K	0.225	Cu	0.441	Zn	0.336
NO <sub>x</sub>	-0.157	NH <sub>4</sub>	-0.435	CaSat	0.318
Mn	-0.151	CEC	0.374	Fe	0.274
CaSat	-0.145	OM	0.372	water table	0.191
MgSat	0.131	P	0.36	P	0.144
NH <sub>4</sub>	-0.096	water table	0.263	Cu	0.07
KSat	0.02	Mn	-0.24	Mn	-0.044

TABLE 24. Pearson's r correlation coefficients between environmental factors and three axes of a principal components analysis of pimple and dune species.

Axis 1: 39 %		Axis 2: 20 %		Axis 3: 13 %	
	r		r		r
B	0.935	K	-0.88	Mn	-0.661
Mg	0.922	KSat	-0.837	CaSat	-0.65
Zn	0.843	NO <sub>x</sub>	-0.813	Cu	0.438
CEC	0.822	CaSat	0.608	Ca	-0.437
Ca	0.816	MgSat	0.526	OM	-0.391
OM	0.698	NH <sub>4</sub>	-0.462	P	0.392
Fe	0.695	CEC	-0.446	Fe	0.372
P	0.558	Mn	-0.31	K	0.336
MgSat	0.517	OM	-0.295	NH <sub>4</sub>	-0.334
NO <sub>x</sub>	-0.508	Ca	-0.263	MgSat	0.315
Cu	0.505	Mg	-0.242	CEC	-0.298
KSat	-0.45	Zn	-0.225	KSat	0.28
water table	0.433	B	-0.217	Mg	-0.233
Mn	-0.309	water table	-0.139	water table	0.167
K	-0.26	Cu	0.12	Zn	0.108
CaSat	0.115	P	0.024	B	-0.074
NH <sub>4</sub>	0.002	Fe	0.018	NO <sub>x</sub>	0.033

TABLE 25. Pearson's  $r$  correlation coefficients between environmental factors and three axes of a Bray-Curtis ordination of pimple species.

Axis 1: 58 %		Axis 2: 17 %		Axis 3: 11 %	
	$r$		$r$		$R$
Salinity	-0.923	KSat	-0.924	NH <sub>4</sub>	-0.732
Mg	-0.651	K	-0.917	O horizon	-0.518
water table	-0.636	CEC	-0.68	elevation	0.372
Elevation	0.537	MgSat	0.476	Mn	0.358
CEC	-0.505	CaSat	0.433	water table	-0.33
B	-0.499	O horizon	-0.404	slope	-0.248
Ca	-0.487	Mg	-0.374	NO <sub>x</sub>	-0.22
Zn	-0.474	B	-0.287	salinity	0.211
Fe	-0.402	Ca	-0.284	Fe	0.187
NO <sub>x</sub>	0.363	Fe	0.272	OM	0.18
East	-0.348	Elevation	0.251	Zn	0.176
P	-0.321	water table	-0.237	MgSat	-0.149
Mn	0.293	NO <sub>x</sub>	0.206	north	-0.147
O horizon	-0.285	Zn	0.189	P	0.145
north	0.266	OM	0.186	Cu	0.122
Cu	-0.265	Slope	-0.17	east	0.101
OM	-0.256	NH <sub>4</sub>	0.136	CEC	0.083
K	-0.145	P	-0.113	CaSat	0.083
CaSat	0.095	North	0.101	Mg	0.084
slope	0.084	Salinity	0.082	Ca	0.081
KSat	-0.069	East	-0.038	KSat	0.065
MgSat	-0.03	Mn	0.005	B	0.066
NH <sub>4</sub>	-0.021	Cu	0.007	K	0.046

TABLE 26. Pearson's r correlation coefficients between environmental factors and three axes of a principal components analysis ordination of pimple species.

Axis 1: 35 %		Axis 2: 17 %		Axis 3: 14 %	
	r		r		R
Ca	-0.962	Fe	-0.802	K	0.88
B	-0.944	OM	-0.779	KSat	0.868
CEC	-0.886	MgSat	-0.768	CaSat	-0.625
Mg	-0.883	Mn	0.747	Zn	-0.603
water table	-0.859	CaSat	0.703	slope	0.475
P	-0.815	North	0.475	Cu	-0.447
elevation	0.779	Salinity	-0.334	CEC	0.41
Zn	-0.67	Elevation	0.32	O horizon	0.4
salinity	-0.667	NO <sub>x</sub>	-0.294	P	-0.335
Cu	-0.658	water table	-0.282	MgSat	-0.225
O horizon	-0.576	East	0.28	salinity	-0.15
NO <sub>x</sub>	0.525	Mg	-0.269	Fe	-0.132
MgSat	0.5	P	0.196	Mg	0.118
K	-0.349	Slope	0.174	B	-0.11
east	-0.307	Ca	0.159	north	-0.09
KSat	-0.289	Zn	-0.12	Ca	-0.086
OM	0.249	O horizon	-0.123	NO <sub>x</sub>	-0.075
CaSat	-0.212	NH <sub>4</sub>	0.097	OM	-0.048
NH <sub>4</sub>	-0.201	B	-0.075	east	0.039
north	0.139	Cu	-0.068	NH <sub>4</sub>	-0.043
slope	0.138	KSat	0.054	elevation	-0.027
Fe	0.11	CEC	-0.026	Mn	0.016
Mn	0.101	K	0.011	water table	-0.016

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### VITA

Brett Allen McMillan grew up in the eastern Tennessee community of Miser Station, near the Great Smoky Mountains. During that time, he was taught to identify many forest trees by his paternal grandfather. After high school, he began his bachelors of arts at Berea College in Berea, Kentucky as a biology major. He worked as a laboratory teaching assistant and learned to enjoy teaching. He was taught to identify even more forest trees by Dr. Ralph Thompson and further developed his appreciation for plants. He graduated with a German minor in 1996, and began a masters of science in the Department of Botany at the University of Florida, Gainesville. For his thesis, he studied the impact of an invasive herb, *Tradescantia fluminensis*, on understory communities of urban forests in and near Gainesville, and became an active member of the Florida Exotic Plant Pest Council. He funded his education by working as a teaching assistant, and his interest in teaching grew. He was taught to identify many Floridian trees and other plants by his colleagues at UF, notably J. Richard Abbot. After completing his MS in 1999, he worked at UF, first as an electron microscopist and then as laboratory manager for the Department of Botany. In 2001, he began work on a PhD in ecological sciences under Dr. Frank Day at the Biology Department of Old Dominion University, Norfolk, Virginia. He worked first as a teaching assistant and then as course coordinator for a large freshman environmental awareness course. He presented papers at several meetings held by the Virginia Academy of Science, Association of Southeastern Biologists, Ecological Society of America, and Botanical Society of America. He was taught to identify many grasses, sedges, and forbs from Hog Island by Dr. Rebecca Bray. Upon completion of his PhD, he plans to teach others to identify plants as a liberal arts professor.