ABSTRACT

A FLORISTIC DESCRIPTION OF A NEOTROPICAL COASTAL SAVANNA IN BELIZE

by

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The diverse graminoid-dominated savannas of Central America remain poorly described. I used percent cover and frequency along line transects and in quadrats to assess the flora, community structure, and environment of a hyperseasonal coastal savanna near Sapodilla Lagoon in Stann Creek District, Belize. The flora consisted of 193 angiosperms, 2 gymnosperms, and 6 pteridophytes, and was dominated by graminoids. Species with the highest importance values were *Mesosetum filifolium*, *Paspalum pulchellum*, *Rhynchospora plumosa*, and *Rhynchospora barbata*. Woody species were scattered in dense clusters throughout the savanna, and were divided into a tall tree layer, dominated by *Pinus caribaea*, and a tree-palm-shrub layer, dominated by *Acoelorrhaphe wrightii* and *Byrsonima crassifolia*. Several large *A. wrightii*-dominated vernal pools were scattered about the landscape marking locations where water breaks through the impenetrable sub-surface. Variation in species composition within the savanna, explored with Non-Metric Multidimensional Scaling (NMDS), correlated strongly with particular species (*A. wrightii* and *P. pulchellum*), topography, cation exchange capacity, and copper concentration. Quantitative comparisons with two other savannas studied in Belize show distinct differences in flora, structure, and dominance in spite of previously being classified as similar.

A Floristic Description of a Neotropical Coastal Savanna in Belize

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Introduction

Savannas are among the most common ecosystems in the world. They are found on every continent except Antarctica, and cover nearly 20% of the earth's terrestrial surface (Cole, 1986). In the Neotropics, savannas are particularly extensive, covering over 2 million km² (Mistry, 2000; Sarmiento, 1983a). Neotropical savannas have various densities of trees, palms and shrubs but the perennial grasses and sedges are always the dominant vegetation (Beard, 1953; Inchausti, 1995; Parsons, 1955; Sarmiento, 1992). In spite of their global and regional importance, an overwhelming interest in Neotropical rainforests has distracted many researchers from the savannas in Central America (but see Furley, 1997).

Savannas are often at a great risk of development. The relatively flat topography, ease of conversion to pasture or cropland, and accessibility to roads and highways, attract new agricultural and industrial development to the lowland savannas. Projected global loss of savannas to various land uses is around 60% by 2100 (Sala *et al.*, 2000). Therefore there is a great need for more in-depth analyses of these important ecological systems.

Agreement on a specific definition of the term "savanna" has been a persistent difficulty. Beard (1953) defined the neotropical savanna as a natural and stable ecosystem occurring under a tropical climate, having a relatively continuous layer of xeromorphic grasses and sedges, and a discontinuous layer of low trees and shrubs. Bourlière and Hadley (1970) added that major growth patterns are closely related to the alternating wet and dry seasons and occasional fires that burn the savanna. Neotropical savannas have an annual cycle that includes a rainy season and a dry season with little or no rain. During the dry season, frequent fires within the savannas maintain openness by reducing the abundance of woody species, and strongly influence vegetation dynamics (Furley, 1997; Kellman and Meave, 1997; Puig, 1972). Sarmiento (1992) states that "fires are an unavoidable consequence of savanna structure and seasonality, and compound the effects of drought and nutrients." Plant available nutrients and moisture may also determine structure and composition of savannas, but in the Neotropics, classifications based on soils have been limited to a small regional scale (Furley 1997; Kellman, 1984; Medina and Silva, 1990). Sarmiento and Monasterio (1975) state that, when savannas are limited to the definition given by Beard, there are still a wide variety of physiognomic types and floristic units under

different climatic, topographic, and soil conditions as well as varying degrees of human interference.

Savannas are widespread throughout Central America and Mexico, and consist of two general types: *hyperseasonal* and *seasonal* (Beard, 1953; Bridgewater *et al.* 2002; Parsons, 1955; Sarmiento, 1983a). Seasonal savannas, as proposed by Sarmiento (1983a), have an annual cycle with a predominantly dry season with frequent fires and a short rainy season. Hyperseasonal savannas also have a predominant dry season, but during the rainy season there is an extended period of water-logging or flooding due to poor soil drainage. Nicaraguan and Honduran savannas cover nearly 25 million acres along the Miskito Coast. Parsons (1955), in his early work on Nicaraguan savannas showed that these vast savannas were actually mosaics, composed of gallery forests, palm thickets, swamps, and shrublands. Puig (1972) differentiated four kinds of savannas in southeastern Mexico: open tree savanna on upper topographic positions with ill-drained lastols, dense wood savannas, “Tasistales” (palm swamps), and “Encinares” (open woodlands of *Quercus oleoides*). Gómez Pompa (1973) identified another costal savanna system in Mexico, which was dominated by the palm *Acoelorrhaphe wrightii* (Arecaceae). Similar variability of savannas has also been identified in Belize, Mexico’s southern neighbor (Bouliere, 1983; Bridgewater *et al.*, 2002; Laughlin, 2002; Woo, 2002).

Belize is located just south of Mexico and east of Guatemala, and has a surface area of approximately 22,963 km² (Meerman and Sabido, 2001). Rainfall in Belize varies from 1347 mm/year in the north to 4526 mm/year in the far south (Hartshorn *et al.*, 1984). The majority of the landscape, stretching along the eastern Caribbean coastline and to the northwest, rises to just under 120 m and is mainly composed of sandy and limestone soils, whereas in the west and southwest the elevation is for the most part between 850 m and 910 m in the Maya Mountains. There are many different community types in Belize; a few of them are: sub-tropical moist forest, inland marsh, sub-tropical deciduous forest, pine forest, and savanna.

The savannas found throughout Belize have been distinguished as two general types (Bridgewater *et al.* 2002; Woo, 2002). The hilltop savannas of Mountain Pine Ridge in the Maya mountains are well-drained seasonal savannas (Meerman and Sabido, 2001). The majority of the savannas, however, are found in the lowlands and are hyperseasonal. These lowland savannas cover approximately 8.8% of the Belizean land surface (Meerman and Sabido, 2001), and are mosaics of broadleaf forests, oak woodlands, pine forests, and palm thickets

(Bridgewater *et al.*, 2002; Parsons, 1955; Sarmiento, 1983a). A recent study of Belizean hyperseasonal savannas suggested a further breakdown of the lowland savannas into *inland lowland* and *coastal lowland savannas* (Woo, 2002).

Although there have been many extensive studies done on the Belizean savannas very few intensive studies are published. In 2000, Woo conducted an intensive floristic and ecological survey of a Belizean savanna. She studied a 1-km² interior, open-woodland hyperseasonal savanna at the Monkey Bay Wildlife Sanctuary in northern Belize. Woo gathered information on the regional flora and variability of vegetation as it related to seasonality, spatial distribution of soil, and topography. In this study, Woo found that the Monkey Bay savanna was made up of 109 taxa in the herb layer, and three woody layers: a broadleaf evergreen and semi-evergreen dominated shrub layer up to 2m in height, a lower tree layer up to 7m of mainly *Calea jamaicensis* and *Gymnopodium floribundum*, and a tall tree layer of *Pinus caribaea*. She found that an elevation gradient, which may be responsible for a flow of nutrients from the northern region to the southern region of the study area, corresponded to a vegetation gradient. She also found phosphorus to be the nutrient most significantly correlated with vegetation (Woo 2002).

The purpose of this study was help fill the void in our knowledge of central America's endangered savannas. Specifically I described the flora of a coastal hyperseasonal savanna in south central Belize, looked for relationships between vegetative composition and environmental parameters, and compared this coastal savanna to the mid-elevation savanna at Monkey Bay Biological Station (Woo, 2002) and the savannas at Rio Bravo Conservation and Management Area (Bridgewater *et al.*, 2002). The field methods used by Woo (2002) at the Monkey Bay Biological Station were replicated to ensure appropriate comparisons between the savannas.

Materials and Methods

Site Description

The study site is a hyperseasonal savanna, approximately 700m by 250m, located west of the All Pines region, in the Stann Creek District of Belize (Figure 1). There are widely scattered *Pinus caribaea*, *Byrsonima crassifolia* and *Curatella americana*, as well as small dense clusters of palms, pines, and broadleaf species. Six vernal pools are scattered around the savanna, the largest of which has a 50-meter radius. Two of the pools have centers consisting of dense mats of *Eleocharis interstincta* and have standing water in them for most of the year. The other pools are shallow with palms, sedges and grasses throughout, and have little to no water in them during the dry season. Evidence of standing water is also seen in the eastern section of the savanna; the grasses in this section have columns of mud approximately 15-25 cm high surrounding the base, and there are land crab holes throughout this area.

Several types of plant communities surround the savanna. The northern side of the study site fades into open-pine woodland that persists for approximately 1 mile north of the open savanna. Beyond this the pines become less frequent as the elevation decreases and vegetation transforms into undescribed hyperseasonal savanna again. Low areas throughout these woodlands have vernal pools as seen in the open savanna.

The western section is bounded by a slow moving creek and a mangrove swamp. Further west, the elevation rises and broadleaf evergreen forest predominates. West of this broadleaf ridge is a short stretch of pine forest and the All Pines savanna. The All Pines savanna is an extensive property of approximately 4452 ha, most of which is hyperseasonal savanna. Local hunters burn this extensive savanna almost yearly.

The southern section ends abruptly in a wall of evergreen broadleaf forest. To the southeast, the savanna integrates with this forest, over the course of a couple hundred meters. Finally the eastern section intermingles with palm and mangrove thickets, vernal pools, and transitions into mangrove swamp up to the edge of the mangrove forest bordering the Sapodilla Lagoon. This last area has standing water over vast portions after heavy rains and during the rainy season.

Data Collection

All data collection occurred in March, May and August 2003. The study site was prepared by marking a perimeter 15 m from the aforementioned edge, and establishing a reference line along a 120° heading across the approximate center of the savanna (Figure 2). Twenty 10m x 50m permanent plots were established in a stratified random arrangement. In each plot corner a steel stake was permanently fixed and coordinates of the plot center were recorded with a Global Positioning Unit (Appendix 1). In each plot, six soil-core samples 4 cm in diameter were taken at each of three depths, 0-10cm, 10-20cm, and 30-40cm for each plot (Figure 3). The six samples from each depth were combined, sealed and analyzed for estimated nitrogen release, weak and strong base, potassium, magnesium, calcium, soil pH, hydrogen, cation exchange capacity, zinc, manganese, iron, copper, and percents of K, Mg, Ca, H, and organic matter (Citrus Research & Education Institute in Dangriga, Belize). Two soil profile pits were dug along the point of reference line, one in the east and one in the west. The approximate distance from the center of each plot to the nearest savanna edge was estimated by walking regular paces; this provided a good estimate of relative distance. Topography, or relative elevation, was recorded using a transit between centers of plots as well as along the perimeter of the study site, marking elevational changes. A total of 56 environmental variables were recorded (18 soil characteristics at 3 depths, distance to edge, and relative elevation).

Several measurements were made on the plants within each 10m x 50m plot. Diameter at breast height (dbh) was measured for all trees, woody shrubs and palms greater than 1.5 m tall and ≥ 1 cm dbh. The line-intercept method was used to record the cover of trees, palms and shrubs along three parallel transects, each 50 m long, arranged along the sides and down the center of each plot (Figure 3). The herbaceous species were studied in four 1m x 1m subplots, two 2.5 m in from the 25 m mark along the edge transects and two along the center transect at 20 and 30 m. Percent cover for each taxon within each 1m x 1m subplot was estimated visually using a cover scale (< 1, 1-5, 6-10, 11-20, 21-40, 41-60, 61-80, 81-100%, Woo, 2002).

The entire savanna was visually inspected during each visit to identify any species that were not represented in the plots. This was carried out by walking approximately regularly spaced transects north to south across the entire site while scanning in an approximate 5m radius, then walking the area again east to west. Species were identified using Gentry (1993), Standley

et al. (1946-77), Stevens *et al.* (2001), and Davidse *et al.* (1994). Nomenclature follows that of Balick *et al.* (2000). Voucher specimens were deposited in the W. S. Turrell Herbarium (MU), and the Belize National Herbarium (BRH) in Belmopan, Belize. Species of Bromeliaceae and CITES-listed families Orchidaceae and Cycadaceae were documented using digital photography in lieu of collection.

Data Analysis

All statistical analyses were conducted using *R* (R Development Core Team, 2004) relying heavily on the *vegan* (Oksanen, 2004) and the *MASS* packages (Venables and Ripley, 2002) for community analyses. The *R* code can be found in Appendix 2.

Overall Savanna Characteristics

The basal area and density of the woody species and palms was calculated using the dbh data. The density of woody species and palms was calculated as the total number of individuals recorded in all main plots (i.e. individuals ha⁻¹).

Absolute cover for herbaceous species in each mainplot was calculated by averaging species cover among subplots within seasons, and then selecting the maximum cover for each species among seasons. For trees, shrubs, and palms the absolute cover data collected from the transect lines, estimated only in August, was totaled among transects. Cover for the woody and herbaceous species were then combined into one data set, and absolute frequency of species was calculated as the percentage of mainplots where the species was present. Relative frequency and relative cover were calculated for each species as absolute value of species *i* divided by the sum of all species values. Importance values in this study are the average of relative frequency and relative cover of combined data. Diversity was calculated in five ways: overall species richness, average species richness per plot, Simpson's index (Lande, 1996), and the exponential form of Shannon's index (Peet, 1974). Percentile confidence intervals were based on 10000 randomizations, resampling main plots with replacement (Davison and Hinkley, 1997).

Variation within the Savanna

Non-Metric Multidimensional Scaling (NMDS) was used to compare mainplots across the savanna. NMDS is a nonparametric dimension reduction technique which avoids the assumption of linear or unimodal response to an underlying gradient (McCune and Grace, 2002). This procedure is the most robust ordination analysis for community data (Grace *et al.*, 2000). I

followed the guidelines provided in McCune and Grace, 2002. NMDS ordinations were based on Bray-Curtis (Sorensen) distances (Faith *et al.*, 1987), selected on the basis of a strong correlation with environmental distances. Prior to calculating the distance matrix, species that were in only one mainplot, i.e. $\leq 5\%$, were removed. The number of dimensions for the study was chosen by conducting stepwise analyses from six dimensions down to one dimension, seeking low stress (McCune and Grace, 2002). Stress is the measure of departure between the distance matrix and the distance in ordination space. Acceptable stress levels for ecological community analysis are below 20%, and below 10% there is virtually no risk of false inference (Clark, 1993; Kruskal, 1964; McCune and Grace, 2002). To test the significance of each number of axes, stress in the observed data was compared to stress from NMDS ordinations of 1000 randomized data sets. Each randomized data set consisted of each species cover values resampled among plots without replacement. The P value was calculated as $(\text{number of stress values from randomized data} + 1)/(1000)$. Proper dimensionality was selected on the basis of stress (Kruskal, 1964), statistical significance, and interpretability (McCune and Grace, 2002). NMDS with the selected dimensionality was repeated on the original data several times and correlation among the resulting configurations tested the stability of the final configuration.

Vector correlations, between an environmental variable and pairs of NMDS axes, were used to find species and environmental relationships with the mainplots in ordination space. Given the large number of possible correlations and the overly conservative nature of Bonferroni adjustments, I selected a reasonably conservative cutoff of $P \leq 0.01$ to identify relevant correlations. Relationships between species and environmental characteristics to NMDS axis scores, Spearman rank correlations were used with Bonferroni adjustments.

Comparison to other savannas

I compared this savanna to the Monkey Bay Savanna (Woo, 2002), Rio Bravo Savanna, and Rio Bravo Forest-Savanna Transition (Bridgewater *et al.*, 2002) using the data provided in those publications. Jaccard's similarity index was used to compare the floras. Where quantitative data was available for species, growth forms, and diversity, the other studies were compared to the confidence intervals from analyses.

Results

Overall Savanna Characteristics

Flora

The savanna was comprised of 193 angiosperms, 2 gymnosperms, and 6 pteridophytes (Table 1). The herbaceous layer was made up of 119 forb and graminoid species, representing 58% of the species. The graminoids included 33 species from the Poaceae and 27 species from the Cyperaceae. The 59 forb species were from 22 different families, and another 23 percent of the flora was made up of woody species, 15 trees and 31 shrubs. The remaining species recorded were *Acoelorrhaphe wrightii* (Palmae), epiphytic orchids and bromeliads, vines, ferns, and parasitic plants. Highest densities of woody species, ferns, epiphytes and vines were found in dense palm thickets, pine groves and broadleaf clusters.

The vertical vegetation structure of the savanna consisted of 5 layers: tall-tree (>6m), tree (6 - 3m), shrub-palm (3 - 1.5m), herbaceous (<1.5 m), and surface. The tall-tree layer was made up of solely *Pinus caribaea*, which was scattered evenly throughout the savanna, had a density of 10 trees per hectare, and a basal area of 1.8 m² ha⁻¹ (Table 2). The tree layer primarily consisted of *Byrsonima crassifolia*, found in 60 % of the plots with a basal area of 0.45 m² ha⁻¹. This layer also included *Curatella americana* and *Chrysobalanus icaco*, species with the next two highest basal areas. Species representing the palm-shrub layer were principally evergreen and semi-evergreen species. Unlike the tree and tall-tree layers, this layer was mainly limited to small dense clusters scattered around the savanna. Vernal pools contained the highest densities of *Acoelorrhaphe wrightii*, the most dense species in this category at 99 individuals/ha. The herbaceous layer was continuous throughout the entire area, with some discontinuity in the palm-shrub thickets. The surface layer was discontinuous and was made up of *Lycopodiella caroliniana*, *Drosera capillaris*, and cyanobacterial mats found around and within palm pools.

Mainplot analyses

Average mainplot richness was 23.55 (95% CI: 20.6 - 26.05) species, ranging from 5 to 36 species. Simpson's diversity was 0.81 (95% CI: 0.75 - 0.85), and the exponential Shannon's was 8.34 (95% CI: 7.78 - 9.85) species equivalents. A total of 90 species were recorded within

the plots. The most important species calculated from transects and subplots was the grass *Mesosetum filifolium*, which had an importance value of only 14.42 (95% CI: 12.17 - 16.58; Table 3). The next most important species was the grass *Paspalum pulchellum*, which had an importance value of 9.72 (95%CI: 8.09 - 11.56; Table 3). The remaining species with importance values ≥ 2 were grasses (*Mesosetum blakei*, *Dichanthelium acuminatum*, *Aristida purpurascens*), sedges (*Rhynchospora plumosa*, *Rhynchospora tenuis*, *Rhynchospora globosa*, *Rhynchospora barbata*), a vine (*Cassytha filiformis*), a palm (*Acoelorrhaphe wrightii*), and two trees (*Byrsonima crassifolia*, *Pinus caribaea*).

Variation within the savanna

Elevation of the mainplots varied from approximately sea level (in one of the vernal pools), to 1.1 m along the northern edge, and on a ridge in the western section. Based on two soil profile pits (Figure 2), I found that approximately 6 dm of mixed sand and organic material covered the underlying clay layer in the western sample, whereas in the eastern sample approximately 1dm of sand with very little organic material covered the clay layer. Iron oxidation (orange and red stained soils) accompanied the shallow the clay layer. A summary of the soil characteristics is in Appendix 3.

Three NMDS axes were identified using our criteria (stress = 6.07%, $P = 0.004$). This stress level suggests that the variation was well described (McCune and Grace, 2002), and Spearman rank correlation between the original the Bray-Curtis distance matrix and the NMDS configuration showed that most of the variation in the original data was explained by the three dimensional NMDS ordination (Spearman $\rho = 0.936$, Figure 4).

The ordination revealed highly significant variation among plots in the importance of five species: *Acoelorrhaphe wrightii*, *Paspalum pulchellum*, *Mesosetum filifolium*, *Rhynchospora globosa* and *Xyris jupicai* (Figures. 5, 6; Tables 4, 5). The soil parameters: medium soil layer Copper (MCu), medium layer cation exchange (MCEC), and medium layer hydrogen (MH) were positively though weakly correlated with the *A. wrightii* gradient (Figure 5). The extreme of this gradient was mainplot #6, which had a monotypic cyperaceous center of *Eleocharis interstincta* and the highest density of palms recorded in the savanna, making it dissimilar to all of the other mainplots. MCEC and MH, in addition to shallow layer Phosphorus (SWBray), deep layer Magnesium (DMg), and deep layer cation exchange capacity (DCEC), were negatively

correlated with the *Paspalum pulchellum* gradient, whereas topography showed strong positive correlation with the gradient. The third axis revealed a gradient represented by the most important species in the savanna, *Mesosetum filifolium*, and another by *Rhynchospora globosa* and *Xyris jupicai* (Figure 6). The *M. filifolium* had no corresponding environmental characteristic supporting it; however, topography was negatively related to *R. globosa* and *X. jupicai*.

Comparison to other savannas

The Sapodilla savanna differed substantially in four ways from two other savannas in Belize, Monkey Bay (Woo 2002) and Rio Bravo (Bridgewater *et al.* 2002): floristic similarity, woody species abundances, growth form composition, and diversity. Monkey Bay and Sapodilla shared 26% of their flora (Jaccard Index of Similarity, $J_S = 0.26$) (Table 6). By contrast Sapodilla savanna and Rio Bravo Savanna shared only 15%. Bridgewater *et al.* (2002) also reported data on *transitional forest-savanna*; this community type had at maximum 5% similarity with the other sites. The flora of the Monkey Bay savanna (Woo 2002) contained 46 species that were not recorded for the Sapodilla savanna. In contrast there were 125 species unique to the Sapodilla savanna, and 150 species unique to the Rio Bravo savannas.

Composition and density of the woody component also differed among the three savannas. The Rio Bravo study reported densities only for *Pinus caribaea*, 76.7 trees/ha, *Quercus oleoides*, 11.6 trees/ha, and for *Curatella americana*, 4.6 trees/ha. The trees and shrubs made up approximately 50% of the flora reported from that study. Woody species were also well represented at the Monkey Bay savanna, comprising 40% of the total flora. Woo (2002) recorded dbh for all trees and shrubs with ≥ 5 cm dbh, which included six of the 33 woody species found there. She found there was a total basal area of 0.51 m²/ha. The highest density she recorded was for *A. wrightii*, 20.2 individuals/ha and *Pinus caribaea* had a density of 14.3 individuals/ha. In the Sapodilla savanna the total basal area of the woody species with dbh ≥ 1 cm was 9.46 m²/ha, for those individuals ≥ 5 cm it was 8.64 m²/ha. The basal area was mainly composed of *A. wrightii* with a basal area of 6.46 m²/ha, and a density of 99 individuals/ha. The next two highest density species at Sapodilla were *P. caribaea* with 10 individuals/ha and *B. crassifolia* with 7 individuals/ha. The woody component of Sapodilla's flora was 23% of the total.

These savannas also differed in their distributions of growth forms (Table 7). The total number of herbaceous species found in the Sapodilla and Rio Bravo savannas was more than twice that of the Monkey Bay site. Nonetheless, the herbaceous floras of both Monkey Bay and Sapodilla were composed of half graminoids and half forbs. The species list for Rio Bravo indicated that there were more than twice as many species of forbs as graminoids. Graminoids at Monkey Bay savanna and at Sapodilla Lagoon savanna were divided evenly between Poaceae and Cyperaceae. The Sapodilla savanna, when compared to the savanna at Rio Bravo, had twice as many graminoid species.

Woo (2002) reported diversity at the Monkey Bay savanna, using the exponential Shannon's index, as 35.3 species equivalents compared to 0.81 (95% CI: 0.75 - 0.85) at Sapodilla. In spite of this apparent difference, the average richness per plot was similar at the two sites (Monkey Bay: average = 26.1; 95% CI: 19.4, 32.8; Sapodilla: average = 23.55; 95% CI: 20.6, 26.05). Because comparable quantitative data was unavailable for Rio Bravo, comparison using this measure of diversity was not possible.

Discussion

The floristic composition recorded at the Sapodilla Lagoon savanna shares characteristics of savanna ecosystems in the Neotropics (Furley, 1997; Parsons, 1955; Sarmiento, 1983a; Taylor, 1963; Woo, 2002). Graminoid dominance in both species diversity and percent cover was an expected result from this study. In addition, two of the most common tree species at Sapodilla, *Byrsonima crassifolia* and *Curatella americana*, are considered indicator species for Neotropical savannas (Huber, 1987). The site had low basal area and percent cover of woody species, typical for neotropical savannas (Beard, 1953). The presence of palm pools was also recorded in descriptions of the Nicaraguan Miskito Coast (Parsons, 1955), as well as savannas described by Puig (1972) in Mexico and Bridgewater *et al.* (2002) in northern Belize, and throughout lowland savannas of Belize (Meerman and Sabido, 2001). *Acoelorrhaphe wrightii*, the primary element of the palm pool, is a common component of all the lowland savannas throughout Belize, and was suggested as an indicator species of Central American savannas by Bridgewater *et al.* (2002).

Soil conditions at Sapodilla are also typical of the Yucatan Peninsula, as reported in Hartshorn *et al.* (1984). The underlying clays are impenetrable to water, so saturation of the coarse sandy soils above occurs rather quickly during a heavy rain. The Sapodilla Lagoon savanna shows evidence for heavy flooding during rain events. The palm pools, when full of water, contain extensive cyanobacterial mats. From September through December the water in the largest pool is continuous with the flooded southeastern section of the savanna. During the dry months, the impenetrable clay layer prevents ground water from rising upward, limiting water availability for most of the savanna, whereas palm pools remain quite moist throughout the dry season. Meerman and Sabido (2001) stated that palm pools remain moist not simply because they retain water but because of water moving upward through cracks in the clay layer.

Compositional differences in the NMDS ordination highlighted several distinct features. The palm pools differ from the drier sites, having high cover of both sedges and palms. *Rhynchospora globosa* (Cyperaceae) was the most dominant species only in plot 17 and grew to approximately 1.5 m tall. There was little similarity between this plot and others throughout the savanna; most others had a graminoid layer that grew only to 1m at most. This difference may

be due to its close proximity to another large palm pool; there was no evidence for extended flooding as seen in palm pools, but soil moistures may be higher in this area due to the palm pool. Another feature was seen in Plot 11, located in the pine woodland on the northern side, was composed mainly of the dominant graminoid layer, but there were far fewer sedges and an increased number of broadleaf and palm clusters. The *Mesosetum filifolium* gradient discovered in the NMDS ordination did not correspond to any measured environmental variable, but since this is the most important species according to calculated importance values, the gradient is important as well.

Topography is likely the most important element of the environmental parameters gathered in this study; a strong correlation between topography and water table is likely. For example, two important middle soil layer characteristics, cation exchange capacity and percent hydrogen, typically increase with increasing soil clay content, and are negatively correlated with topography. Excavation of two soil pits suggest that topography appeared most related to the thickness of the sand layer covering the clay layer. Soil drainage in sandy soils is higher than in soils with high amounts of clay, thus the sand layer may be providing habitat for species that are less suited to saturated soils. A vegetation gradient explained by topography was represented by positive correlation with *Paspalum pulchellum*, and negatively correlated with *Rhynchospora globosa* and *Xyris jupicai*. Topography on large scale may not be such an interesting parameter of study when comparing the lowland savannas; however, there are considerable correlations at the local scale where small differences may reflect biologically important gradients in key soil characteristics.

Studies that have collected data on temporal changes in savanna vegetation have shown that this may lead to a better measure of biodiversity in these sites (José and Fariñas, 1991; Sarmiento, 1983b). I was not able to test temporal variation of species relative cover in wet season vs. dry in this study, due to an intentionally set fire set 15 days prior to the wet season data collection trip. The study site, as mentioned before, was selected because it is relatively remote and few people utilize the surrounding areas, and thus had a lower risk of fire. The nearby property of All Pines was sold to a foreign-owned development corporation in the summer of 2003. In Belize it is common for surveying crews to burn savannas and understory of woodlands to simplify the search for property markers. The corporation was completing a property survey during December of 2003, and consequently fires burned the study site. Another

savanna that burned in the summer of 2003 was the Monkey Bay savanna (Woo 2002). By that time, most of the interior-lowland savannas had already burned, including the All Pines savanna.

Monkey Bay savanna contained more pronounced shrub and tree layers than the Sapodilla savanna, in spite of little differences in our data in woody species cover. The basal area of large trees and shrubs was a bit greater than that of the Sapodilla Lagoon site and there were twice as many woody species found there. Woo's study (2002) only recorded dbh for those individuals with ≥ 5 cm dbh. This left out a large portion of the woody vegetation in the savanna. Another survey at the Monkey Bay site, including those individuals with ≥ 1 cm dbh, would yield a much higher total basal area.

In spite of large differences between Monkey Bay and Sapodilla in the total number of species and the percent of woody species cover, the growth form distributions of the herbaceous flora were strikingly similar. The herbaceous flora at both sites was evenly split between forbs and graminoids, and the graminoids were evenly split between the Poaceae and the Cyperaceae. These ratios have not been previously reported for Central American hyperseasonal savannas, and suggest common factors controlling both sites. The use of such ratios may be useful in classification of savannas throughout Central America, and warrant further examination. The Jaccard index showed only 26% similarity between the floras of these two sites. This difference, in addition to an increased woody component, illustrates the dissimilarity between the Sapodilla lowland coastal savanna and the Monkey Bay interior lowland savanna.

Although Meerman and Sabido (2001) classified the savannas of Rio Bravo, Monkey Bay and Sapodilla as *short grass savanna with shrubs*, this study showed substantial differences in the density of both trees and shrubs in addition to variations in species composition among the three sites. Further baseline research needs to be done within the interior lowland savannas, as seen at Monkey Bay and Rio Bravo, as well as within the coastal lowland savannas, such as at Sapodilla savanna. This research would provide quantitative results to compare with published qualitative descriptions of the Belizean savannas, further strengthening savanna classification.

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Figure 1. Map of Belize and enlarged map of the Sapodilla Lagoon savanna site. Asterisks indicate the locations of the savannas. Large map from Director General of Military, listed in Literature Cited.

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Figure 2. Generalized site diagram of mainplot layout and point of reference line. The two black stars indicate locations of profile pits. Not to Scale.

Figure 3. Diagram of an individual 10 X 50m quadrat with four 1 · 1m nested subplots, three horizontal 50m transects, and 6 points of soil extraction (*). Note: not to scale. Redrawn from Woo 2002.

Figure 4. Plots of the Bray-Curtis Dissimilarity Matrix vs. distance between points in NMDS. Three dimensions altogether, explaining approximately 94% of the variation.

Figure 5. First and second axes in the ordination. Numbers represent the plots seen in the site map (Figure 2). Arrows are significant gradient vectors correlated with plots. Values in Table 4 are the correlation coefficients and level of significance for the vectors shown in the ordination. Special notation on vectors: *Paspalum pulchellum* (Pasppulc); *Acoelorrhaphe wrightii* (Acoewrig); *Xyris jupicai* (Xyrijupi); Topography (Topo); Medium Layer Cation Exchange Capacity (MCEC); Medium Layer Copper (Mcu); Medium Layer Hydrogen (MH); Shallow Layer Weak Bray (SWBray); Deep Layer Cation Exchange Capacity (DCEC); Deep Layer Magnesium (DMg).

Figure 6. Second and third axes in the ordination. Numbers represent the plots seen in the site map (figure Map). Arrows are significant gradient vectors correlated with plots. Values in Table 5 are the correlation coefficients and level of significance for the vectors shown in the ordination. Special notation on the vectors: *Rhynchospora globosa* (Rhynglob); *Xyris jupicai* (Xyrijupi); *Paspalum pulchellum* (Pasppulc); *Mesosetum filifolium* (Mezofili); Topography (Topo).

Table 1. Species List for Sapodilla Lagoon Savanna

FERNS

Blechnaceae

Blechnum serrulatum Rich.

Dennstaedtiaceae

Lindsaea lancea (L.) Bedd.

Pteridium caudatum (L.) Maxon

Lycopodiaceae

Lycopodiella caroliniana (L.) Pic.Serm.

Lycopodiella cernua (L.) Pic.Serm.

GYMNOSPERMS

Pinaceae

Pinus caribaea Morelet var. *hondurensis* (Seneclauze) W.H.Barrett & Golfari

Zamiaceae

Zamia polymorpha D.W.Stev., A.Moretti & L. Gaudio

ANGIOSPERMS

Anacardiaceae

Metopium brownei (Jacq.) Urb.

Annonaceae

Xylopia frutescens Aubl.

Apocynaceae

Mandevilla subsagittata (Ruiz & Pav.) Woodson

Rhabdadenia biflora (Jacq.) Müll.Arg.

Araceae

Syngonium angustatum Schott

Asteraceae

Calea jamaicensis (L.) L.

Calea longipedicellata B.L. Rob. & Greenm.

Bignoniaceae

Amphitecna breedloveii A.H.Gentry

Bromeliadaceae

Tillandsia spp.

Burmanniaceae

Burmannia capitata (Walter ex J.F. Gmel.) Mart.

Chrysobalanaceae

Chrysobalanus icaco L.

Hirtella racemosa Lam.

Clusiaceae

Symphonia globularis L.f.

Combretaceae

Conocarpus erecta L.

Convolvulaceae

Evolvulus sericeus Sw.

Merremia aturensis (H.B.K.) Hallier f.

Cyperaceae

Bulbostylis junciformis (H.B.K.) C.B. Clarke

Cyperus haspan L.

Eleocharis geniculata (L.) Roem. & Schult.

Eleocharis interstincta (Vahl) Roem. & Schult.

Fuirena camptotricha C. Wright

Lagenocarpus guianensis Nees

Rhynchospora barbata (Vahl.) Kunth

Rhynchospora cephalotes (L.) Vahl

Rhynchospora chapmanii M.A. Curtis

Rhynchospora curvula Griesb.

Rhynchospora elliottii A. Dietrich

Rhynchospora fascicularis (Michx.) Vahl. subsp. *fascicularis*

Rhynchospora filifolia A. Gray

Rhynchospora globosa (H.B.K.) Roem. & Schult.

Rhynchospora globularis (Chapm.) Small var. *recognita* Gale

Rhynchospora harperi Small

Rhynchospora holoschoenoides (Rich.) Herter

Rhynchospora oligantha A. Gray var. *oligantha*

Rhynchospora plumosa Elliott

Rhynchospora pusilla Chapm. ex M.A. Curtis

Rhynchospora rugosa (Vahl) Gale

Rhynchospora tenuis Link

Rhynchospora sp.
Scleria bracteata Cav.
Scleria ciliata Michx.
Scleria georgiana Core
Scleria tenella Kunth

Dilleniaceae

Curatella americana L.
Davilla kunthii A.St.Hil.

Dioscoreaceae

Dioscorea matagalpensis Uline ?

Droseraceae

Drosera capillaris Poir.

Eriocaulaceae

Eriocaulon sp.

Erythroxylaceae

Erythroxylum guatamalense Lundell

Euphorbiaceae

Pera arborea Mutis

Fabaceae

Aeschynomene histrix Poir. var. *incana* (Vogel) Benth.
Aeschynomene paniculata Willd. ex Vogel
Chamaecrista desvauxii (Collad.) Killip var. *mollissima* (Benth.) H.S. Irwin & Barneby
Chamaecrista diphylla (L.) Greene
Chamaecrista hispidula (Vahl) H.S.Irwin & Barneby
Chamaecrista kunthiana (Schltdl. & Cham.) H.S.Irwin & Barneby
Chamaecrista nictitans (L.) Moench
Clitoria falcata Lam.
Desmodium barbatum (L.) Benth. & Oerst.
Gliricidia sp.
Inga pinetorum Pittier
Macroptilium gracile (Poepp. ex Benth.) Urb.
Senna hayesiana (Britton & Rose) H.S.Irwin & Barneby
Stylosanthes guianensis (Aubl.) Sw.
Tephrosia nitens Benth.
Zornia reticulata Sm.

Fagaceae

Quercus oleoides Schltdl. & Cham.

Gentianaceae

Coutoubea spicata Aubl.

Schultesia guianensis (Griesb.) Benth. & Hook.f. ex Hemsl.

Iridaceae

Alophia spicata (Loes.) Goldblatt

Lamiaceae

Hyptis atrorubens Poit.

Hyptis brevipes Poit.

Hyptis conferta Pohl ex Benth.

Hyptis lantanifolia Poit.

Marsypianthes chamaedrys (Vahl) Kuntze

Lauraceae

Cassytha filiformis L.

Lentibulariaceae

Utricularia hispida Lam.

Utricularia juncea Vahl

Utricularia subulata L.

Loranthaceae

Oryctanthus cordifolius (C.Presl) Urb.

Oryctanthus spicatus (Jacq.) Eichler

Struthanthus cassythoides Millsp. ex Standl.

Malphigiaceae

Byrsonima crassifolia (L.) H.B.K.

Malvaceae

Sida linifolia Cav.

Melastomataceae

Acisanthera crassipies (Naudin) Wurdack

Acisanthera quadrata Pers.

Clidemia capitellata (Bonpl.) D.Don

Clidemia novemnervia (DC) Triana

Clidemia sericea D.Don

Miconia albicans (Sw.) Triana
Miconia ciliata (Rich.) DC
Nepsera aquatica (Aubl.) Naudin
Tococa guianensis Aubl.

Myricaceae

Myrica cerifera L.

Myrsinaceae

Myrsine floridana A.DC

Myrtaceae

Chamguava gentlei (Lundell) Landrum var. *gentlei*
Myrcia splendens (Sw.) DC
Psidium guineense Sw.

Ochnaceae

Ouratea nitida (Sw.) Engl.
Sauvagesia erecta L.

Onagraceae

Ludwigia octovalvis (Jacq.) P.H.Raven

Orchidaceae

Brassavola nodosa (L.) Lindl.
Spp. Many Sterile

Oxalidaceae

Oxalis frutescens L. subsp. *angustifolia* (H.B.K.) Lourteig

Palmae

Acoelorrhaphe wrightii (Griesb. & H.Wendl.) H.Wendl. ex Becc.

Passifloraceae

Passiflora foetida L.

Poaceae

Andropogon gerardii Vitman
Andropogon glomeratus (Walter) Britton, Sterns & Poggenb.
Andropogon leucostachyus H.B.K.
Andropogon virginicus L.
Aristida purpurascens Poir. var. *tenuspica* (Hitchc.) Allred
Aristida tinctoria Trin. & Rupr.

Axonopus aureus P.Beauv.
Axonopus purpusii (Mez) Chase
Dichantherium aciculare (Desv. ex Poir.) Gould & C.A.Clark var. *ramosum* (Griesb.)
 Davidse
Dichantherium acuminatum (Sw.) Gould & C.A.Clark var. *longiligulatum* (Nash) Gould &
 C.A.Clark
Dichantherium strigosum (Muhl. ex Elliott) Freckmann var. *strigosum*
Dichantherium sp.
Echinolaena gracilis Swallen
Eragrostis elliotii S.Watson
Hypogynium virgatum (Desv.) Dandy
Leptochloa virgata (L.) P.Beauv.
Leptocoryphium lanatum (H.B.K.) Nees
Mesosetum blakei Swallen
Mesosetum filifolium F.T. Hubb.
Panicum caricoides Nees ex Trin.
Panicum laxum Sw.
Panicum stenodes Griesb.
Panicum tenerum Beyr. ex Trin.
Panicum tuerckheimii Hack.
Paspalum pectinatum Nees ex Trin.
Paspalum pulchellum Kunth
Paspalum serpentinum Hochst. ex Steud.
Paspalum sp.
Sacciolepis myuros (Lam.) Chase
Schizachyrium sanguineum (Sw.) Nees ex Buse
Thrasya campylostachya (Hack.) Chase
Trachypogon spicatus (L.f.) Kuntze
Tripsacum latifolium Hitchc.

Polygalaceae

Polygala aparinoides Hook. & Arn.
Polygala hygrophila H.B.K.
Polygala incarnata L.
Polygala leptocaulis Torr. & A.Gray
Polygala longicaulis H.B.K.
Polygala variabilis H.B.K.

Polygonaceae

Coccoloba sp.

Rhizophoraceae

Cassipourea elliptica (Sw.) Poir

Rubiaceae

Amaioua corymbosa H.B.K.

Chomelia protracta (Bartl. ex DC) Standl.

Coccocypselum guianense (Aubl.) K.Schum.

Diodia apiculata (Willd. ex Roem. & Schult.) K.Schum.

Guettarda combsii Urb.

Palicourea triphylla DC

Psychotria fruticetorum Standl.

Psychotria graciliflora Benth.

Psychotria hoffmannseggiana (Willd. ex Roem. & Schult.) Müll.Arg.

Psychotria nervosa Sw.

Psychotria poeppigiana Müll.Arg.

Richardia scabra L.

Spermacocce suaveolens (G.Mey.) Kuntze

Spermacocce tenuior L.

Sapindaceae

Matayba apetala (Macfad.) Radlk.

Sapotaceae

Chrysophyllum cainito L.

Scrophulariaceae

Agalinis harperi Pennell

Angelonia ciliaris B.L.Rob.

Bacopa lacertosa Standl.

Buchnera pusilla H.B.K.

Simaroubaceae

Simarouba glauca DC

Smilacaceae

Smilax velutina Killip & C.V.Morton

Smilax sp.

Solanaceae

Schwenkia americana L.

Sterculiaceae

Melochia nodiflora Sw.

Symplocaceae

Symplocos martinicensis Jacq.

Turneraceae

Piriqueta cistoides (L.) Griseb.

Turnera aromatica Arbo

Turnera pumilea L.

Verbenaceae

Citharexylum caudatum L.

Tamonea spicata Aubl.

Viscaceae

Phoradendron quadrangulare (H.B.K.) Krug & Urb.

Xyridaceae

Xyris ambigua Beyr. ex Kunth.

Xyris jupicai Rich.

Table 2. Woody species frequency, density and basal area.

Species	Total # of individuals	Frequency (% of plots)	Density(trees/ha)	BA/ha
<i>Pinus caribaea</i>	10	25	10	1.80
<i>Curatella americana</i>	5	15	5	0.01
<i>Byrsonima crassifolia</i>	55	60	55	0.45
<i>Acoelorrhaphe wrightii</i>	99	65	99	6.87
<i>Erythroxylum guatemalense</i>	5	15	5	0.00
<i>Citharexylum caudatum</i>	2	10	2	0.00
<i>Chrysobalanus icaco</i>	7	5	7	0.23
<i>Myrsine floridana</i>	5	10	5	0.02
<i>Amphitecna breedlovei</i>	8	10	8	0.01
<i>Symplocos martinicensis</i>	3	10	3	0.01
<i>Chomelia protracta</i>	4	5	4	0.00
<i>Simarouba glauca</i>	1	5	1	0.00
<i>Symphonia globularis</i>	2	10	2	0.01
<i>Pera arborea</i>	2	5	2	0.02
<i>Inga pinetorum</i>	1	5	1	0.01
<i>Ouratea nitida</i>	4	5	4	0.00
<i>Cassipourea elliptica</i>	3	5	3	0.01
<i>Guettarda combsii</i>	2	5	2	0.00
<i>Matayba apetala</i>	1	5	1	0.00
<i>Coccoloba sp.</i>	3	5	3	0.00
<i>Psychotria graciliflora</i>	4	5	4	0.02

Table 3. Species Relative Cover, Relative Frequency and Importance Values with 95% Confidence Intervals. Calculated from mainplot and transect cover data.

Taxa	Rel Cover	Rel Freq	IV	Lwr 95% CI	Upr 95% CI
<i>Mesosetum filifolium</i>	24.82	4.04	14.43	12.17	16.58
<i>Paspalum pulchellum</i>	15.41	4.04	9.73	8.09	11.56
<i>Rhynchospora plumosa</i>	11.57	4.04	7.80	6.65	8.99
<i>Rhynchospora barbata</i>	7.10	4.04	5.57	4.41	6.87
<i>Mesosetum blakei</i>	4.53	2.77	3.65	2.25	5.17
<i>Cassytha filiformis</i>	2.96	4.04	3.50	3.16	3.85
<i>Dichanthelium acuminatum</i>	3.09	3.40	3.25	2.36	3.99
<i>Byrsonima crassifolia</i>	1.82	4.04	2.93	2.44	3.37
<i>Acoelorrhaphe wrightii</i>	2.35	3.19	2.77	1.86	3.92
<i>Rhynchospora tenuis</i>	2.55	2.98	2.76	1.91	3.46
<i>Rhynchospora globosa</i>	4.45	0.85	2.65	0.31	5.42
<i>Pinus caribaea</i>	2.47	2.13	2.30	1.01	3.70
<i>Aristida purpurascens</i>	0.83	3.19	2.01	1.48	2.59
<i>Lycopodiella caroliniana</i>	1.83	2.13	1.98	1.11	3.01
<i>Drosera capillaris</i>	0.34	3.40	1.87	1.47	2.22
<i>Hypogynium virgatum</i>	1.14	2.34	1.74	1.06	2.43
<i>Paspalum serpetinum</i>	1.83	1.28	1.55	0.57	3.05
<i>Xyris jupicai</i>	0.90	2.13	1.52	0.86	2.16
<i>Scleria georgiana</i>	0.35	2.55	1.45	0.96	1.91
<i>Myrica cerifera</i>	0.13	2.55	1.34	0.91	1.78
<i>Axonopus purpusii</i>	0.85	1.70	1.28	0.61	1.94
<i>Acisanthera quadrata</i>	0.17	2.34	1.25	0.77	1.73
<i>Eleocharis interstincta</i>	2.23	0.21	1.22	0.00	3.96
<i>Sauvagesia erecta</i>	0.19	2.13	1.16	0.70	1.55
<i>Curatella americana</i>	0.23	1.91	1.07	0.53	1.59
<i>Dichanthelium strigosum</i>	0.34	1.70	1.02	0.51	1.57
<i>Rhynchospora curvula</i>	0.96	1.06	1.01	0.25	1.92
<i>Chamaecrista nictitans</i>	0.37	1.06	0.71	0.23	1.37
<i>Dichanthelium aciculare</i>	0.10	1.28	0.69	0.24	1.14
<i>Merremia aturensis</i>	0.02	1.28	0.65	0.22	1.08
<i>Polygala spp.</i>	0.02	1.28	0.65	0.22	1.13
<i>Utricularia subulata</i>	0.03	1.28	0.65	0.22	1.11
<i>Angelonia ciliaris</i>	0.17	1.06	0.62	0.22	1.16
<i>Andropogon leucostachyus</i>	0.36	0.85	0.61	0.11	1.19
<i>Evolvulus sericeus</i>	0.05	1.06	0.56	0.21	1.01
<i>Utricularia hispida</i>	0.03	1.06	0.56	0.21	0.97
<i>Leptocoryphium lanatum</i>	0.27	0.85	0.56	0.12	1.08
<i>Panicum tenerum</i>	0.27	0.85	0.55	0.11	1.09
<i>Thrasya campylostachya</i>	0.15	0.85	0.50	0.12	0.97
<i>Erythroxylum guatamalense</i>	0.14	0.85	0.49	0.11	0.92
<i>Piriqueta cistoides</i>	0.05	0.85	0.46	0.11	0.85

<i>Chomelia protracta</i>	0.26	0.64	0.45	0.00	0.95
<i>Trachypogon spicatus</i>	0.23	0.64	0.45	0.00	1.01
<i>Chamaecrista kunthiana</i>	0.06	0.85	0.44	0.11	0.86
<i>Clidemia sp.</i>	0.02	0.85	0.44	0.11	0.82
<i>Gliricidia sp.</i>	0.04	0.85	0.44	0.11	0.83
<i>Burmannia capitata</i>	0.02	0.85	0.44	0.10	0.90
<i>Rhynchospora rugosa</i>	0.20	0.64	0.42	0.00	0.90
<i>Melochia nodiflora</i>	0.02	0.64	0.33	0.00	0.70
<i>Cassipourea elliptica</i>	0.07	0.43	0.25	0.00	0.60
<i>Clidemia sericea</i>	0.07	0.43	0.25	0.00	0.65
<i>Myrsine floridana</i>	0.07	0.43	0.25	0.00	0.59
<i>Passiflora foetida</i>	0.07	0.43	0.25	0.00	0.58
<i>Rhynchospora chapmanii</i>	0.07	0.43	0.25	0.00	0.61
<i>Calea longipedicellata</i>	0.04	0.43	0.23	0.00	0.58
<i>Chrysobalanus icaco</i>	0.25	0.21	0.23	0.00	0.71
<i>Ouratea nitida</i>	0.01	0.43	0.23	0.00	0.57
<i>Schwenkia americana</i>	0.04	0.43	0.23	0.00	0.61
<i>Chamaecrista diphylla</i>	0.02	0.43	0.22	0.00	0.56
<i>Chamaecrista desvauxii</i>	0.14	0.21	0.18	0.00	0.55
<i>Coccoloba sp.</i>	0.10	0.21	0.16	0.00	0.45
<i>Guettarda combsii</i>	0.08	0.21	0.15	0.00	0.43
<i>Symphonia globularis</i>	0.08	0.21	0.15	0.00	0.43
<i>Bulbostylis junciformis</i>	0.07	0.21	0.14	0.00	0.44
<i>Inga pinetorum</i>	0.06	0.21	0.14	0.00	0.40
<i>Pera arborea</i>	0.07	0.21	0.14	0.00	0.41
<i>Smilax sp.</i>	0.06	0.21	0.14	0.00	0.41
<i>Rhynchospora sp.</i>	0.04	0.21	0.13	0.00	0.40
<i>Simarouba glauca</i>	0.05	0.21	0.13	0.00	0.39
<i>Amaioua corymbosa</i>	0.02	0.21	0.12	0.00	0.34
<i>Cyperus rotundus</i>	0.04	0.21	0.12	0.00	0.40
<i>Hirtella racemosa</i>	0.04	0.21	0.12	0.00	0.37
<i>Macroptilium gracile</i>	0.04	0.21	0.12	0.00	0.39
<i>Scleria tenella</i>	0.02	0.21	0.12	0.00	0.38
<i>Spermacoce suaveolens</i>	0.02	0.21	0.12	0.00	0.34
<i>Zamia polymorpha</i>	0.05	0.21	0.12	0.00	0.40
<i>Blechnum serrulatum</i>	0.02	0.21	0.11	0.00	0.37
<i>Buchnera pusilla</i>	0.00	0.21	0.11	0.00	0.36
<i>Chamguava gentlei</i>	0.00	0.21	0.11	0.00	0.33
<i>Clidemia novemnervia</i>	0.01	0.21	0.11	0.00	0.32
<i>Paspalum pectinatum</i>	0.00	0.21	0.11	0.00	0.33
<i>Tamonea spicata</i>	0.00	0.21	0.11	0.00	0.35
Unknown 1	0.00	0.21	0.11	0.00	0.33
Unknown 3	0.00	0.21	0.11	0.00	0.34
Sum	100.00	100.00			

Table 4. Vector correlations of species and environmental characteristics with NMDS Axes 1 & 2.

Species	r²	P-value
<i>Paspalum pulchellum</i>	0.63	0.001
<i>Acoelorrhaphe wrightii</i>	0.85	0.001
<i>Xyris jupicai</i>	0.54	0.001
Env	r²	P-value
Topography	0.53	0.001
Shallow layer weak Bray	0.56	0.005
Medium layer Copper	0.73	0.001
Medium layer cation exchange capacity	0.87	0.005
Medium layer Hydrogen	0.80	0.002
Deep layer cation exchange capacity	0.56	0.003
Deep layer Magnesium	0.48	0.001

Table 5. Vector correlations of species and environmental characteristics with NMDS Axes 2 & 3.

Species	r²	p-value
<i>Mesosetum filifolium</i>	0.59	<0.001
<i>Paspalum pulchellum</i>	0.64	<0.001
<i>Xyris jupicai</i>	0.51	0.003
<i>Rhynchospora globosa</i>	0.63	<0.001
Env	r²	P-value
Topography	0.55	0.001

Table 6. Fraction of flora shared between pairs of sites using Jaccard's index. Abbreviated for Rio Bravo Savanna (a), Rio Bravo Forest-Savanna Transition (b).

Savannas	Monkey Bay	Sapodilla	Rio Bravo (a)	Rio Bravo (b)
Monkey Bay	1			
Sapodilla	0.26	1		
Rio Bravo (a)	0.19	0.15	1	
Rio Bravo (b)	0.05	0.04	0.01	1

Table 7. Comparison of vegetation types at Monkey Bay, Sapodilla Lagoon, and both sites from Rio Bravo combined.

	Monkey Bay	Sapodilla Lagoon	Rio Bravo
% Herbs	60	59	41
% Woody	40	23	50
Number of Species			
Tree	13	15	45
Vine	5	10	18
Shrub	20	31	83
Herbs	49	119	106
Woody	33	46	128
Total	109	199	258
Number of Species in Herbaceous Category			
Graminoids	20	60	29
Sedges	10	27	11
Grasses	10	33	18
Forbs	29	59	82

APPENDIX I.

Global Positions of Main Plots			
Plot code	Plot #	Latitude	Longitude
1-1L	1	N 16° 45.839'	W 88° 19.865'
1-1R	2	N 16° 45.801'	W 88° 19.886'
1-2L	3	N 16° 45.865'	W 88° 19.848'
1-2R	4	N 16° 45.791'	W 88° 19.892'
2-1L	5	N 16° 45.821'	W 88° 19.841'
2-1R	6	N 16° 45.789'	W 88° 19.862'
2-2L	7	N 16° 45.853'	W 88° 19.823'
2-2R	8	N 16° 45.769'	W 88° 19.875'
3-1L	9	N 16° 45.808'	W 88° 19.814'
3-1R	10	N 16° 45.789'	W 88° 19.829'
3-2L	11	N 16° 45.852'	W 88° 19.790'
3-2R	12	N 16° 45.764'	W 88° 19.843'
4-1L	13	N 16° 45.787'	W 88° 19.798'
4-1R	14	N 16° 45.763'	W 88° 19.804'
4-2L	15	N 16° 45.803'	W 88° 19.784'
4-2R	16	N 16° 45.731'	W 88° 19.832'
5-1L	17	N 16° 45.778'	W 88° 19.770'
5-1R	18	N 16° 45.763'	W 88° 19.776'
5-2L	19	N 16° 45.815'	W 88° 19.746'
5-2R	20	N 16° 45.742'	W 88° 19.793'

APPENDIX II.

Computational Code for R.

```
veg <- read.csv("RAWHERBNOWOOD.csv")
dim(veg)

#### MAIN PLOT COVER HERBS
# This gives max mainplot percent cover among seasons of each species cover, based
on averages among subplots.
# Thus mpave will NOT have "subplots" as a variable, reducing the number of cols
by 1
# aggregate works just like tapply, but on all columns of a defined data.frame
mpave <- aggregate(veg[,5:65], list(veg$MP,veg$Section,veg$Date), mean)
dim(mpave)
# aggregate renames the variables
mpave[,1:5]
# Rename vars
names(mpave)[1:3] <- c("MP","Section","Date")
# This will grab just the max among seasons, reducing the # of cols by 1
mpmaxave <- aggregate(mpave[,4:64], list(mpave$MP,mpave$Section), max)
mpmaxave[,1:5]
# Rename vars
names(mpmaxave)[1:2] <- c("MP","Section")
mpmaxave[,1:4,1:4]
#Created a function (x) to calculate the sum of the cover for each plot then divided
the absolute value of cover for each species(the max for all seasons) by this new sum.
# "Apply to the cover values in each row a function that divides each by the total
cover."
# Transpose because R applies the function to each row as a vector, then joins up
each vector as columns, by default
dim(mpmaxave) # shows 20 plots as rows, two independent vars and 93 species

#### MAIN PLOT COVER WOODY SPECIES
## Woody relative cover per plot
# Totaling the cover along the three transects for each plot
wood <- read.csv("Tree cover.csv")
dim(wood)
summary(wood)
totcovwood <- aggregate(wood[,4:26], list(wood$MP,wood$Section), sum)
totcovwood[,1:4]
dim(totcovwood)

#### MAIN PLOT IMPORTANCE PERCENTAGES
```



```

# Importance Percentages = the mean of relative cover and relative frequency
# cbind combines the cover data from herbs and shrubs,
# Idid the same for the frequency from herb and shrubs,
# then calculated for the Importance values.

a <- cbind( mpmaxave, totcovwood[,3:25])
dim(a)
str(a[,1:5])
a[1:4,1:4]
#####BOOTSTRAP SAVANNA WIDE CI'S AT THE MAIN PLOT LEVEL
## MAKE EXPERIMENTAL UNIT THE MAINPLOT SO FREQUENCY IS THE
NUMBER OF MAINPLOTS IN WHICH A SPECIES IS OBSERVED.
#### NOW BOOTSTRAP RANDOM DATA FROM THE COVER MATRIX
## Generate r random 20 x S matrices of vegetation data
# resulting in an array of dimension 20 x S x r
# This resamples mp
dim(a)
spp <- as.matrix(a[,3:dim(a)[2]])
class(spp)
dim(spp)
r <- 1000
S <- dim(spp)[2];S
rdat <- array(dim=c(20,S,r))
dim(rdat)
for(i in 1:r) rdat[,i] <- { spp[sample(1:20, 20, replace=T),] } # spp must be a matrix,
otherwise this doesn't work.
dim(rdat);length(rdat)

#####Calculate the IV and Relative etc.. for the whole savanna.
quercus <- cbind( mpmaxave, totcovwood[,3:25])
alba <- t( apply(quercus[,3:86], 1, function(x) length(x[x>0])/length(x) *100))

awhole <- t(apply(a[,3:86],2, sum))
awholerel <- t(apply(awhole,1, function(x) x/sum(x)*100))
awholerel
bwhole <- t(apply(a[,3:86],2, function(x) length(x[x>0])/20*100))
bwhole
bwholere1 <- t(apply(bwhole,1, function(x) x/sum(x)*100))
bwholere1
write.table(awholerel, file="Relative Cover.csv", sep="," , col.names=NA)
write.table(bwholere1, file="Relative Frequency.csv", sep="," , col.names=NA)

# Function to calculate relative cover of each species across the savanna based on a
20 X 80+ cover maxtrix
F.relcov <- function(X) { #where X is a dataframe or matrix
  a <- apply( X, 2, sum)

```

```

100 * a/sum(a) }
sum(F.relcov(spp)) # a check on it

# Function to calculate relative frequency of each species across the savanna based on
a 20 X 80+ cover maxtrix
F.relfreq <- function(X) { a <- apply(X, 2, function(x) sum(x>0) )
100 * a / sum(a) }
sum(F.relfreq(spp)) # a check
## calculate relative cover of all 20 plots
rdrmat <- matrix(0,nrow=r,ncol=S) # a holder for all r relative densities of S species
for(i in 1:r) rdrmat[i,1:S] <- {F.relcov(rdat[,i])}
rdobs <- F.relcov(spp)
rfrmat <- matrix(0,nrow=r, ncol=S)
for(i in 1:r) rfrmat[i,1:S] <- {F.relfreq(rdat[,i])}
rfobs <- F.relfreq(spp)

IVrmat = (rdrmat+rfrmat)/2
dim(IVrmat)
IVobs = (rdobs +rfobs)/2
IVobs
IV <- function(data) {rdobs <- F.relcov(data)
rfobs <- F.relfreq(data)
IV <-(rdobs +rfobs)/2
IV}
IVobs - IV(spp)
sum(IV(spp))
##put the original spp names back on!
colnames(IVrmat) <- colnames(spp)

## Sort the species columns from most to least important
IVsort <- {
a1 <- rbind(1:dim(spp)[2],apply(IVrmat,2,mean))
b<- a1[,rev(order(a1[2,]))]
IVrmat[,b[1,]]}

CIs <- t(apply(IVsort,2,function(x) {
L95CL <- quantile(x,0.025)
U95CL <- quantile(x, 0.975)
c(L95CL, Mean=mean(x), U95CL)} ) )
LCLplotval <- CIs[,1]
LCLplotval[CIs==0] <- 0.01
IV.table <- round(cbind(CIs[,1:2],IV.obs=rev(sort(as.vector(IVobs))),CIs[,3]),2);
IV.table

write.table(IV.table, file="IVtable.csv", sep="," , col.names=NA)
sum(CIs[,2])

```

```

plot(1:S,CIs[,2], ylim=c(0.01,50 ),pch=19,log="y")
arrows(1:S,CIs[,2], 1:S, LCLplotval, angle=90, length=0.1)
arrows(1:S, CIs[,2], 1:S, CIs[,3], angle=90, length=0.1)
lines(1:dim(spp)[2], rev(sort(as.vector(IVobs))), col="red", lty=2)

#### ALPHA DIVERSITY
# shannon
#H = -sum p_i log(b) p_i, where p_i is the proportional abundance of species i and b
is the base of the logarithm. It is most popular to use natural logarithms, but some
argue for base b = 2
sw <- function(x){x <- x[x>0]
  exp(- sum( x/sum(x) * log(x/sum(x)) ))}

shannon <- apply(spp,1, sw)
shannon
sw(apply(spp, 2, sum) )
shanndf <- data.frame(mp=1:20, div =shannon);shanndf
summary(shannon)
library(boot)
boot.ci(boot(shannon,function(x,i) {mean(x[i])},R=1000))

# Simpson's estimate of diversity
# This will calculate Simpson's diversity index (Lande 1996) for each main plot
across all seasons
dim(spp)
simpson <- apply(spp,1,
  function(x) {1 - sum( (x/sum(x))^2 )})
simpdf <- data.frame(mp=1:20, div =simpson);simpdf
summary(simpson)

## Perform "by hand" percentile confidence intervals (to my mind the most intuitive
sort).
rmeans <- numeric(10000)
for(i in 1:10000) rmeans[i] <- mean(simpson[sample(1:20, 20, replace=T)])
quantile(rmeans, 0.025);quantile(rmeans, 0.975)
write.table(simpson, file="SPSimpson.csv", sep=",", col.names = NA)
dim(a)

library(mva)
library(vegan)
## Species richness (S), per plot basis
S <- specnumber(spp) ## rowSums(BCI > 0) does the same...
S
rmean.S <- numeric(10000)
for(i in 1:10000) rmean.S[i] <- mean(S[sample(1:20,20, replace=TRUE)])
quantile(rmean.S, 0.025);quantile(rmean.S, 0.975)

```

```

write.table(S, file="Species Richness.csv", sep="," , col.names = NA)
## Deleting species from cover calculations that were in less than 2 of mainplots
## This is less than 5% of the sample units
str(a[,1:4])
str(spp[,1:4])
a <- t(apply(spp,1,function(x) x/sum(x)))
dim(a)
apply(a,1,sum)
allcolnos <- 1:dim(spp)[2]
colsincluded <- allcolnos[apply(a,2,function(x) length(x[x>0])>1)]
colsincluded
vegtrimmed <- a[,colsincluded]; vegtrimmed
layout(matrix(1:4,nrow=2, byrow=TRUE))
barplot( table(apply(a,2, function(x) length(x[x>0]))) ) # Is this a graph of the number
species (y axis) found in a given number of plots (x axis), i.e. a species-occupancy
distribution?
text(6,20, "Note bimodality.")
barplot( table(apply(vegtrimmed,2, function(x) length(x[x>0]))) )

# THIS GIVES SHORTENS THE NAMES OF THE SPECIES INTO AN 8
Character NAME
colnames(vegtrimmed) <- make.cepnames(colnames(vegtrimmed))
dim(vegtrimmed)
vegtrimmed[1:4,1:4]

## DISSIMILARITY INDEX AS A MEASURE OF DISTANCE IN
MULTIDIMENSIONAL SPACE
## the Importance values used here are based on MainPlot data and
# reflect Max cover and Max frequency for each of the species throught
# all of the seasons.
library(vegan)
env <- read.csv("env.csv")
rankindex(scale(env[,2:57]),vegtrimmed, method="spearman")# WHAT DO THE
NUMBERS REPRESENT?#
rankindex
# transform data with Bray-Curtis index,
# this is commonly refered to Sorensen's index as well
brayveg <- vegdist(vegtrimmed,method="bray")
brayveg # Bray-Curtis Distance Matrix, expressed as percentages#
plot(brayveg)
hist(brayveg)

## NON-METRIC MULTIDIMENSIONAL SCALING
## The recommended way of running NMDS (Minchin 1987)
library(MASS) ## isoMDS

```

```

library(mva) ## cmdscale: default start to isoMDS
library(vegan)
# Get the baseline solution: start with cmdscale
mds.null6 <- isoMDS(brayveg,k=6, maxit=1000, tol=1e-7)
mds.null5 <- isoMDS(brayveg,k=5, maxit=1000,tol=1e-7)
mds.null4 <- isoMDS(brayveg,k=4, maxit=1000,tol=1e-7)
mds.null3 <- isoMDS(brayveg,k=3, maxit=1000,tol=1e-7)
mds.null2 <- isoMDS(brayveg,k=2, maxit=1000,tol=1e-7)
mds.null1 <- isoMDS(brayveg,k=1, maxit=1000,tol=1e-7)

## Finding the proper number of dimentions
# This is where multiple runs of the data will be done in NMS stepping down from 6
dimentions to 1.
# 6 Dimentions
mod6 <- replicate(10, isoMDS(brayveg, initMDS(brayveg,k=6), maxit=1000,k=6,
trace=FALSE, tol=1e-7),simplify=FALSE)
length(mod6)
mod6.stress <- sapply(mod6, function(x) x$stress); mod6.stress
mod6.best <- mod6[[which.min(mod6.stress)]]
mod6.best

#####THE MONTECARLO TEST BELOW.
# The test randomizes (rearranges) observed species abundances among plots for each
species.
# Thus, the observed abundances are all preserved, but rearranged into different plots.
## The folloing provides 1000 NMS runs on different randomized sets of
vegtrimmed, with 1000 iterations, and 6 dimensions
rvt6 <- matrix(NA,nrow=20,ncol=dim(vegtrimmed)[2])
rstress6 <- replicate(1000, {for(i in 1:dim(vegtrimmed)[2]) rvt6[,i] <-
sample(vegtrimmed[,i],size=20)
      for(i in 1:dim(vegtrimmed)[1]) rvt6[i,] <- rvt6[i,]/sum(rvt6[i,])
      brayveg6 <- vegdist(rvt6,method="bray")
      mds.r6 <- isoMDS(brayveg6,k=6,trace=FALSE,
maxit=1000,tol=1e-7)
      mds.r6$stress})
P=(1+length(rstress6[rstress6<=mod6.best$stress]))/(1+length(rstress6))
P

# 5 Dimentions
mod5 <- replicate(10, isoMDS(brayveg, initMDS(brayveg,k=5), maxit=1000,k=5,
trace=FALSE, tol=1e-7),simplify=FALSE)
length(mod5)
mod5.stress <- sapply(mod5, function(x) x$stress); mod5.stress
mod5.best <- mod5[[which.min(mod5.stress)]]
mod5.best

```

```
## The folloing provides 1000 NMS runs on different randomized sets of
vegtrimmed, with 1000 iterations, and 5 dimensions
rvt5 <- matrix(NA,nrow=20,ncol=dim(vegtrimmed)[2])
rstress5 <- replicate(1000, {for(i in 1:dim(vegtrimmed)[2]) rvt5[,i] <-
sample(vegtrimmed[,i],size=20)
      for(i in 1:dim(vegtrimmed)[1]) rvt5[i,] <- rvt5[i,]/sum(rvt5[i,])
      brayveg5 <- vegdist(rvt5,method="bray")
      mds.r5 <- isoMDS(brayveg5,k=5,trace=FALSE,
maxit=1000,tol=1e-7)
      mds.r5$stress})
P=(1+length(rstress5[rstress5<=mod5.best$stress]))/(1+length(rstress5))
P
```

```
# 4 Dimentions
mod4 <- replicate(10, isoMDS(brayveg, initMDS(brayveg,k=4), maxit=1000,k=4,
trace=FALSE, tol=1e-7),simplify=FALSE)
length(mod4)
mod4.stress <- sapply(mod4, function(x) x$stress); mod4.stress
mod4.best <- mod4[[which.min(mod4.stress)]]
mod4.best
```

```
## The folloing provides 1000 NMS runs on different randomized sets of
vegtrimmed, with 1000 iterations, and 4 dimensions
rvt4 <- matrix(NA,nrow=20,ncol=dim(vegtrimmed)[2])
rstress4 <- replicate(1000, {for(i in 1:dim(vegtrimmed)[2]) rvt4[,i] <-
sample(vegtrimmed[,i],size=20)
      for(i in 1:dim(vegtrimmed)[1]) rvt4[i,] <- rvt4[i,]/sum(rvt4[i,])
      brayveg4 <- vegdist(rvt4,method="bray")
      mds.r4 <- isoMDS(brayveg4,k=4,trace=FALSE,
maxit=1000,tol=1e-7)
      mds.r4$stress})
P=(1+length(rstress4[rstress4<=mod4.best$stress]))/(1+length(rstress4))
P
```

```
# 3 Dimentions
mod3 <- replicate(10, isoMDS(brayveg, initMDS(brayveg,k=3), maxit=1000,k=3,
trace=FALSE, tol=1e-7),simplify=FALSE)
length(mod3)
mod3.stress <- sapply(mod3, function(x) x$stress); mod3.stress
mod3.best <- mod3[[which.min(mod3.stress)]]
mod3.best
```

```
## The folloing provides 50 NMS runs on different randomized sets of vegtrimmed,
with 1000 iterations, and 3 dimensions
rvt3 <- matrix(NA,nrow=20,ncol=dim(vegtrimmed)[2])
```

```

rstress3 <- replicate(1000, {for(i in 1:dim(vegtrimmed)[2]) rvt3[,i] <-
sample(vegtrimmed[,i],size=20)
      for(i in 1:dim(vegtrimmed)[1]) rvt3[i,] <- rvt3[i,]/sum(rvt3[i,])
      brayveg3 <- vegdist(rvt3,method="bray")
      mds.r3 <- isoMDS(brayveg3,k=3,trace=FALSE,
maxit=1000,tol=1e-7)
      mds.r3$stress})
P=(1+length(rstress3[rstress3<=mod3.best$stress]))/(1+length(rstress3))
P

```

```

# 2 Dimentions
mod2 <- replicate(10, isoMDS(brayveg, initMDS(brayveg,k=2), maxit=1000,k=2,
trace=FALSE, tol=1e-7),simplify=FALSE)
length(mod2)
mod2.stress <- sapply(mod2, function(x) x$stress); mod2.stress
mod2.best <- mod2[[which.min(mod2.stress)]]
mod2.best

```

The folloing provides 50 NMS runs on different randomized sets of vegtrimmed, with 1000 iterations, and 2 dimensions

```

rvt2 <- matrix(NA,nrow=20,ncol=dim(vegtrimmed)[2])
rstress2 <- replicate(1000, {for(i in 1:dim(vegtrimmed)[2]) rvt2[,i] <-
sample(vegtrimmed[,i],size=20)
      for(i in 1:dim(vegtrimmed)[1]) rvt2[i,] <- rvt2[i,]/sum(rvt2[i,])
      brayveg2 <- vegdist(rvt2,method="bray")
      mds.r2 <- isoMDS(brayveg2,k=2,trace=FALSE,
maxit=1000,tol=1e-7)
      mds.r2$stress})
P=(1+length(rstress2[rstress2<=mod2.best$stress]))/(1+length(rstress2))
P

```

```

# 1 Dimentions
mod1 <- replicate(10, isoMDS(brayveg, initMDS(brayveg,k=1), maxit=1000,k=1,
trace=FALSE, tol=1e-7),simplify=FALSE)
length(mod1)
mod1.stress <- sapply(mod1, function(x) x$stress); mod1.stress
mod1.best <- mod1[[which.min(mod1.stress)]]
mod1.best

```

The folloing provides 50 NMS runs on different randomized sets of vegtrimmed, with 1000 iterations, and 1 dimensions

```

rvt1 <- matrix(NA,nrow=20,ncol=dim(vegtrimmed)[2])
rstress1 <- replicate(1000, {for(i in 1:dim(vegtrimmed)[2]) rvt1[,i] <-
sample(vegtrimmed[,i],size=20)

```

```

        for(i in 1:dim(vegtrimmed)[1]) rvt1[i,] <- rvt1[i,]/sum(rvt1[i,])
        brayveg1 <- vegdist(rvt1,method="bray")
        mds.r1 <- isoMDS(brayveg1,k=1,trace=FALSE,
maxit=1000,tol=1e-7)
        mds.r1$stress})
P=(1+length(rstress1[rstress1<=mod1.best$stress]))/(1+length(rstress1))
P

#Plot to find the proper number of dimensions.
# couldn't find the easy way to do this
q <- min(rstress6)
r <- min(rstress5)
s <- min(rstress4)
t <- min(rstress3)
u <- min(rstress2)
v <- min(rstress1)

f <- max(rstress6)
g <- max(rstress5)
h <- max(rstress4)
i <- max(rstress3)
j <- max(rstress2)
k <- max(rstress1)

l <- mean(rstress6)
m <- mean(rstress5)
n <- mean(rstress4)
o <- mean(rstress3)
p <- mean(rstress2)
p1 <- mean(rstress1)

# making x, y data for plotting
stress <-
c(mod6.best$stress,mod5.best$stress,mod4.best$stress,mod3.best$stress,mod2.best$stress,mod1.best$stress)
minr <- c(q,r,s,t,u,v)
maxr <- c(f,g,h,i,j,k)
meanr <- c(l,m,n,o,p,p1)
dimensions <- c(6,5,4,3,2,1)

#scree plotting the data
plot(dimensions, maxr,col="Blue",ylim=c(0,max(maxr)))
points(dimensions, stress)
points(dimensions, minr,col="Red")
points(dimensions, meanr,col="Purple")

```



```

# GOING WITH 3 DIM MODEL
# 3 Dimentions
mod3a <- replicate(10, isoMDS(brayveg, initMDS(brayveg,k=3), maxit=1000,k=3,
trace=FALSE, tol=1e-7),simplify=FALSE)
length(mod3a)
mod3a.stress <- sapply(mod3a, function(x) x$stress); mod3a.stress
mod3a.best <- mod3a[[which.min(mod3a.stress)]]
mod3a.best

# 3 Dimentions
mod3b <- replicate(10, isoMDS(brayveg, initMDS(brayveg,k=3), maxit=1000,k=3,
trace=FALSE, tol=1e-7),simplify=FALSE)
length(mod3b)
mod3b.stress <- sapply(mod3b, function(x) x$stress); mod3b.stress
mod3b.best <- mod3b[[which.min(mod3b.stress)]]
mod3b.best

mod3.best=postMDS(mod3.best,brayveg, halfchange=F)
mod3a.best=postMDS(mod3a.best,brayveg, halfchange=F)
mod3b.best=postMDS(mod3b.best,brayveg, halfchange=F)

pairs(cbind(mod3.best$points,mod3a.best$points,mod3b.best$points))

## Getting the proportion of variation explained by each axis, using the r^2
# between distance in ordination space and distance in the original space.
## A check on the NMDS procedure and my number of dimensions selected. This
plot was seen on labdsv website,
# then I used their function code to get the plot.
library(labdsv)
layout(matrix(1:6,nrow=2,byrow=T))
# axes 1&2
z <- mod3a.best$points[,1:2]
a <- orddist(z, 1)
plot(brayveg,a, xlab="Computed Distance(Bray/Curtis)", ylab="NMDS Distance")
text(min(brayveg),max(a), paste("r =",format(cor(brayveg,a),digits=3)), pos=4)
# axes 2&3
z <- mod3a.best$points[,2:3]
a <- orddist(z, 1)
plot(brayveg,a, xlab="Computed Distance(Bray/Curtis)", ylab="NMDS Distance")
text(min(brayveg),max(a), paste("r =",format(cor(brayveg,a),digits=3)), pos=4)
# all axes
z <- mod3a.best$points
a <- orddist(z, 1)
plot(brayveg,a, xlab="Computed Distance(Bray/Curtis)", ylab="NMDS Distance")
text(min(brayveg),max(a), paste("r =",format(cor(brayveg,a),digits=3)), pos=4)

```

```

# Plot of the three dimensional ordination axes 1 &2
plot(mod3a.best$points[,1:2], type = "n", xlab="Dim1")
text(mod3a.best$points[,1:2], labels = as.character(1:nrow(vegtrimmed)))

# Plot of the three dimensional ordination axes 2 &3
plot(mod3a.best$points[,2:3], type = "n", xlab="Dim1")
text(mod3a.best$points[,2:3], labels = as.character(1:nrow(vegtrimmed)))

## correlations of the environmental factors with the points from each axis
# getting the env cors
envcor12<- envfit(mod3a.best, env[,2:57],choices=c(1,2), 1000); envcor12
envcor23<- envfit(mod3a.best, env[,2:57],choices=c(2,3), 1000); envcor23

# getting the spp cors
spcora <- envfit(mod3a.best, vegtrimmed,choices=c(1,2), 1000);spcora
spcorb <- envfit(mod3a.best, vegtrimmed,choices=c(2,3), 1000);spcorb

# plot of NMDS axes one and two with significant (p<.01)species and env
correlations
plot(mod3a.best$points[,1],mod3a.best$points[,2], type = "n", xlab="Axis 1",
ylab="Axis 2")
text(mod3a.best$points[,1:2], labels = as.character(1:nrow(vegtrimmed)))
plot.envfit(envcor12, p.max= 0.01,col="dark green",cex=.8, arrow.mul=5)
plot.envfit(spcora, p.max=0.01, col="red",cex=.8, arrow.mul=5)

# plot of NMDS axes two and three with significant (p<.01)species and env
correlations
plot(mod3a.best$points[,2],mod3a.best$points[,3], type = "n", xlab="Axis 2",
ylab="Axis 3")
text(mod3a.best$points[,2:3], labels = as.character(1:nrow(vegtrimmed)))
plot.envfit(envcor23, p.max= 0.01, col="dark green",cex=.8, arrow.mul=5)
plot.envfit(spcorb, p.max=0.01, col="red",cex=.8, arrow.mul=5)

highlight.corr<- function(m, min.corr=0.44, simplify=TRUE){
# This assumes your matrix of correlations has row and column names
m[m < 0.44] <- 0
if(simplify==TRUE) {
cols.in <- apply(m, 2, function(x) any(x >= min.corr) )
rows.in <- apply(m, 1, function(x) any(x >= min.corr) )
round(m[rows.in,cols.in],2)}
else if(simplify==FALSE) m
}

# Summary of Environmental Data
tite <- summary(env)
write.table(tite, file="summary env.csv", sep="," , col.names = NA)

```

```

# Species vs. Env
test <- cor(env,vegtrimmed,method="spearman");highlight.corr(test)
test1 <- cor(env,mod3a.best$points, method="spearman"); highlight.corr(test1)
test2 <- cor(vegtrimmed,mod3a.best$points, method="spearman");
highlight.corr(test2)

## Starting to compare woo IV data to our IV data
# Use Jaccard index to compare. A high value will express high similarity.
compare <- read.csv("FLORALCOMPARE.csv")
dim(compare)
compare <- t(compare)
#this compares the savannas from Monkey Bay, Sapodilla Lagoon, Rio Bravo
Savanna, and Rio Bravo Transition
similar <- 1-vegdist(compare[2:5,2:384], method="jaccard")

```

APPENDIX III.

Summary table of Soil Characteristics from the three depths (Part 1 of 4).
Special notation in this section: Estimated Nitrogen Release (ENR), Weak Bray (Weak Bray Test), Strong Bray (Strong Bray Test).

Depth	Soil Characters				
Shallow	Organic Material %	ENR lbs/A	Weak Bray ppm	Strong Bray ppm	K ppm
	Min. :1.600	Min. : 76.0	Min. :2.00	Min. :3.0	Min. :14.00
	1st Qu.:2.500	1st Qu.: 94.0	1st Qu.:2.00	1st Qu.:3.0	1st Qu.:16.00
	Median :3.150	Median :107.0	Median :2.00	Median :4.0	Median :17.50
	Mean :3.375	Mean :111.5	Mean :2.35	Mean :3.8	Mean :18.65
	3rd Qu.:3.775	3rd Qu.:119.5	3rd Qu.:3.00	3rd Qu.:4.0	3rd Qu.:20.25
	Max. :6.700	Max. :178.0	Max. :4.00	Max. :6.0	Max. :26.00
Medium	Organic Material %	ENR lbs/A	Weak Bray ppm	Strong Bray ppm	K ppm
	Min. :0.600	Min. : 55.00	Min. :1.0	Min. :2.00	Min. : 8.00
	1st Qu.:0.800	1st Qu.: 60.00	1st Qu.:1.0	1st Qu.:2.00	1st Qu.: 8.00
	Median :0.950	Median : 63.00	Median :1.0	Median :2.50	Median :10.00
	Mean :1.180	Mean : 67.55	Mean :1.4	Mean :2.75	Mean :11.10
	3rd Qu.:1.325	3rd Qu.: 70.50	3rd Qu.:2.0	3rd Qu.:3.00	3rd Qu.:12.25
	Max. :4.000	Max. :124.00	Max. :2.0	Max. :5.00	Max. :19.00
Deep	Organic Material %	ENR lbs/A	Weak Bray ppm	Strong Bray ppm	K ppm
	Min. :0.300	Min. :48.00	Min. :1.00	Min. :2.00	Min. :11.00
	1st Qu.:0.400	1st Qu.:50.00	1st Qu.:1.00	1st Qu.:2.00	1st Qu.:15.75
	Median :0.500	Median :53.00	Median :1.00	Median :2.00	Median :18.00
	Mean :0.615	Mean :55.15	Mean :1.05	Mean :2.15	Mean :17.70
	3rd Qu.:0.625	3rd Qu.:55.75	3rd Qu.:1.00	3rd Qu.:2.00	3rd Qu.:20.00
	Max. :2.200	Max. :88.00	Max. :2.00	Max. :3.00	Max. :23.00

Summary table of Soil Characteristics from the three depths (Part 2 of 4).
Special notation in this section is: Cation Exchange Capacity (CEC).

Shallow	CEC meq/100g	%K	%Mg	%Ca	%H
	Min. :1.300	Min. :0.800	Min. : 7.50	Min. :12.60	Min. :26.90
	1st Qu.:1.475	1st Qu.:2.575	1st Qu.:11.40	1st Qu.:26.15	1st Qu.:51.42
	Median :1.500	Median :2.900	Median :12.40	Median :28.55	Median :55.30
	Mean :1.790	Mean :2.925	Mean :12.59	Mean :29.49	Mean :55.09
	3rd Qu.:1.700	3rd Qu.:3.225	3rd Qu.:14.03	3rd Qu.:31.10	3rd Qu.:60.40
	Max. :5.600	Max. :4.200	Max. :16.30	Max. :57.20	Max. :75.60
Medium	CEC meq/100g	%K	%Mg	%Ca	%H
	Min. :0.90	Min. :1.10	Min. : 8.20	Min. :20.10	Min. :32.60
	1st Qu.:1.20	1st Qu.:1.70	1st Qu.:10.00	1st Qu.:24.45	1st Qu.:46.95
	Median :1.20	Median :1.90	Median :11.10	Median :29.35	Median :54.90
	Mean :1.45	Mean :2.06	Mean :12.48	Mean :31.13	Mean :53.44
	3rd Qu.:1.50	3rd Qu.:2.20	3rd Qu.:13.20	3rd Qu.:36.35	3rd Qu.:60.88
	Max. :4.60	Max. :3.70	Max. :25.60	Max. :48.80	Max. :67.00
Deep	CEC meq/100g	%K	%Mg	%Ca	%H
	Min. :1.400	Min. :0.600	Min. :17.90	Min. :18.90	Min. : 7.50
	1st Qu.:2.600	1st Qu.:1.200	1st Qu.:28.02	1st Qu.:24.02	1st Qu.:36.23
	Median :3.000	Median :1.600	Median :30.80	Median :27.80	Median :39.90
	Mean :3.235	Mean :1.505	Mean :31.32	Mean :29.09	Mean :38.06
	3rd Qu.:3.500	3rd Qu.:1.700	3rd Qu.:34.95	3rd Qu.:34.00	3rd Qu.:43.92
	Max. :6.400	Max. :2.100	Max. :44.90	Max. :49.90	Max. :49.10

Summary table of Soil Characteristics from the three depths (Part 3 of 4).

Shallow	Mg ppm	Ca ppm	pH	H meq/100g
	Min. :13.00	Min. : 70	Min. :4.100	Min. :0.40
	1st Qu.:21.50	1st Qu.: 80	1st Qu.:4.700	1st Qu.:0.80
	Median :23.00	Median : 90	Median :4.900	Median :0.80
	Mean :26.65	Mean : 98	Mean :4.815	Mean :1.03
	3rd Qu.:27.50	3rd Qu.:110	3rd Qu.:4.900	3rd Qu.:1.00
	Max. :73.00	Max. :170	Max. :5.300	Max. :4.20
Medium	Mg ppm	Ca ppm	pH	H meq/100g
	Min. : 10.0	Min. : 60.0	Min. :4.60	Min. :0.400
	1st Qu.: 15.0	1st Qu.: 60.0	1st Qu.:4.90	1st Qu.:0.600
	Median : 18.0	Median : 80.0	Median :5.00	Median :0.700
	Mean : 24.4	Mean : 87.5	Mean :4.99	Mean :0.775
	3rd Qu.: 23.0	3rd Qu.: 90.0	3rd Qu.:5.10	3rd Qu.:0.800
	Max. :140.0	Max. :230.0	Max. :5.30	Max. :2.200
Deep	Mg ppm	Ca ppm	pH	H meq/100g
	Min. : 36.00	Min. : 60	Min. :4.7	Min. :0.300
	1st Qu.: 94.75	1st Qu.:130	1st Qu.:4.9	1st Qu.:1.000
	Median :111.00	Median :160	Median :5.0	Median :1.200
	Mean :124.70	Mean :188	Mean :5.1	Mean :1.195
	3rd Qu.:149.50	3rd Qu.:225	3rd Qu.:5.1	3rd Qu.:1.450
	Max. :250.00	Max. :450	Max. :6.4	Max. :2.000

Summary table of Soil Characteristics from the three depths (Part 4 of 4).

Shallow	Zn ppm	Mn ppm	Fe ppm	Cu ppm
	Min. :0.100	Min. :1.0	Min. : 30.0	Min. :0.800
	1st Qu.:0.300	1st Qu.:1.0	1st Qu.: 48.5	1st Qu.:1.000
	Median :0.600	Median :2.0	Median : 62.5	Median :1.200
	Mean :0.645	Mean :1.8	Mean : 66.7	Mean :1.165
	3rd Qu.:0.825	3rd Qu.:2.0	3rd Qu.: 72.5	3rd Qu.:1.225
	Max. :1.500	Max. :4.0	Max. :161.0	Max. :2.000
Medium	Zn ppm	Mn ppm	Fe ppm	Cu ppm
	Min. :0.100	Min. :1.00	Min. :14.00	Min. :0.70
	1st Qu.:0.200	1st Qu.:1.00	1st Qu.:18.00	1st Qu.:0.90
	Median :0.500	Median :1.00	Median :19.00	Median :1.20
	Mean :0.515	Mean :1.55	Mean :24.75	Mean :1.26
	3rd Qu.:0.725	3rd Qu.:2.00	3rd Qu.:25.25	3rd Qu.:1.50
	Max. :1.600	Max. :4.00	Max. :71.00	Max. :2.90
Deep	Zn ppm	Mn ppm	Fe ppm	Cu ppm
	Min. :0.100	Min. :1.00	Min. : 11.00	Min. :0.900
	1st Qu.:0.275	1st Qu.:1.00	1st Qu.: 15.50	1st Qu.:1.000
	Median :0.550	Median :1.00	Median : 18.00	Median :1.300
	Mean :0.575	Mean :2.00	Mean : 32.50	Mean :1.410
	3rd Qu.:0.800	3rd Qu.:2.25	3rd Qu.: 25.25	3rd Qu.:1.525
	Max. :1.800	Max. :6.00	Max. :219.00	Max. :4.200