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Plant Species Richness and Species Area Relationships in a Florida Sandhill

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Plant Species Richness and Species Area Relationships in a Florida Sandhill Community

by

Monica Ruth Downer

A thesis submitted in partial fulfillment
Of the requirements for the degree of
Master of Science
Department of Biology
College of Arts and Sciences
University of South Florida

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autocorrelation

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TABLE OF CONTENTS

List of Tables	ii
List of Figures	iv
Abstract	v
Chapter One: Introduction	1
Pine Sandhill Communities	1
Optimal fire-frequency for prescribed burns within pine sandhill communities: an ongoing debate	2
Past and future research on pine sandhill	7
Species area curves: A quick background	8
Debate on the best mathematical function for the species area curve	10
The role of scale in species area curves	12
How species area curves can be used to examine plant species richness in pine sandhill	13
Spatial autocorrelation and the relationship between species composition and abiotic factors	13
Objectives and what we hope to accomplish	14
Chapter Two: Methods	15
Study site	15
Data collection	15
Data analysis	17
Chapter Three: Results	20
Species occurrence and distribution of richness	20
Linearity of the species area curves and similarity of richness among burn plots	22
Jaccard dissimilarity and the effects of physical distance, burn regime and elevation on compositional similarity among burn plots	26
Effect of elevation on species richness within burn plots	28
Chapter Four: Discussion	30
Species occurrence and distribution of richness	30
Linearity of the species area curves and similarity of richness among burn plots	30

Jaccard dissimilarity and the effects of physical distance, burn regime and elevation on compositional similarity among burn plots	32
Conclusions	34
References cited	36
Appendices	40
Appendix A: Extra Tables	41

LIST OF TABLES

Table 1: Slopes and intercepts for all linear fits.....	24
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LIST OF FIGURES

Figure 1: Four general sampling schemes of species area curves	9
Figure 2: GIS map of burn plots within the University of South Florida Ecological Research Area [ERA].....	6
Figure 3: Illustration of quadrat & transect spacing.....	17
Figure 4: Rank species occurrence over study area	20
Figure 5: Distribution of richness per quadrat.....	21
Figure 6: Species area curve based on species richness calculated from all possible combinations of quadrats.....	22
Figure 7: Species area curves for all each burn treatment.....	23
Figure 8. Illustration of intercepts and slopes of the best fit linear regressions for richness	24
Figure 9: Best fit linear model for plot 1E (Durbin-Watson).....	25
Figure 10: Mantel correlograms for Jaccard dissimilarity vs. distance alone (left) and Jaccard dissimilarity vs. distance, holding treatment constant (right)	27
Figure 11: Mantel correlograms for Jaccard dissimilarity vs. distance alone (left) and Jaccard dissimilarity vs. distance, holding elevational difference constant (right).....	27
Figure 12: Species richness in each burn plot, as a function of elevation contour	29

ABSTRACT

Pine sandhill are integral pyrogenic communities in the southeastern United States. Though once widespread, habitat destruction, fire suppression and fragmentation have reduced the population to nearly 3%. It is important to learn as much as possible about these unique areas in order to implement best management practices to conserve and restore the existing populations of these communities.

Fire is central to the maintenance of pine sandhill communities and two conceptual hypothesis regarding burn frequency have come to light in maintaining the unique species composition and richness of these areas. The first is the Intermediate Disturbance Hypothesis which suggests that intermediate fire regime maintains species diversity. The second is the Most Frequent Fire Hypothesis suggests that these areas should be burned as frequently as fuels allow.

We used species area curves and species area relationships to answer the following questions about a pine sandhill community in the burn plot area of the University of South Florida Ecological Research Area (ERA). What are the patterns of species richness and how do they change with spatial scale? What are the factors contributing to the heterogeneity of this area and how much are they contributing? Do similarly burned areas have similar species composition? Do our results shed some light on the Intermediate Disturbance Hypothesis or Most Frequent Fire Hypothesis?

We found that physical distance contributed more to species compositional and spatial patterns than burn regime or elevation, whose effects were small. On this particular scale, the results did not support either the Intermediate Disturbance Hypothesis or Most Frequent Fire Hypothesis, as acquisition rates of species in all burn regimes were quite similar. There was no obvious pattern of increased species richness with frequent or intermediate burning.

Our results suggest a need for a dynamic plan for the conservation, preservation and management of pine sandhill communities. One must consider as many factors as possible when managing these lands, as every sandhill is unique. More research should be conducted on these ecologically sensitive and diminished areas in order to formulate best management practices to conserve, protect and restore pine sandhill in the southeastern United States.

INTRODUCTION

Pine sandhill communities

Pine sandhill communities are important communities in Florida and the Southeastern United States. Sandhill provides essential habitat for many rare and endemic plant and animal species. Gopher tortoise (*Gopherus polyphemus*) and southeastern pocket gopher (*Geomys pinetis*) are especially important keystone species within sandhills as their burrows are utilized by 60 or more species of vertebrates and 300 species of invertebrates (FNAI 2010). Peninsular Florida sandhills support many rare plant species including scrub pigeon-wing (*Clitoria fragrans*), Florida toothache-grass (*Ctenium floridanum*), longspurred mint (*Dicerandra cornutissima*), giant orchid (*Pteroglossaspis ecristata*), scrub stylisma (*Sylisma abdita*), variable-leaf crownbeard (*Verbesisna heterophylla*), and clasping warea (*Warea amplexifolia*) (FNAI 2010). Sandhill communities also are important for aquifer recharge because the porous sand allows for water to percolate rapidly with little runoff and minimal evaporation (FNAI 2010).

Pine sandhill is characterized by widely spaced pine trees with a sparse midstory of deciduous oaks and a moderate to dense groundcover of herbs, grasses and low shrubs. Sandhill occurs along the rolling topography and deep sands of the Southeastern U.S. Coastal Plain (FNAI 2010). The canopy is dominated by longleaf pine (*Pinus palustris*) with an intermittent subcanopy layer of smaller pines and hardwoods. Shrub cover varies from sparse to dense and includes species such as dwarf huckleberry (*Gaylussacia*

dumosa), running oak (*Quercus ellioti*), gallberry (*Ilex glabra*) and Darrow's blueberry (*Vaccinium darrowii*). Herbaceous cover varies according to the effects of shading and density of the shrubs. Wiregrass (*Aristida stricta*) is often dominant, but a large diversity of grasses and forbs can be present. Forbs typically found include narrowleaf silkgrass (*Pityopsis graminifolia*), pineland silkgrass (*Pityopsis aspera*), goldenrod (*Solidago spp.*), squarehead (*Tetragonotheca helianthoides*), soft greeneyes (*Berlandiera pumila*), and *Liatris* species. A diverse group of legumes is often present including sensitive briar (*Mimosa quadrivalvis*), sidebeak pencil flower (*Stylosanthes biflora*), and goat's rue (*Tephrosia virginiana*), along with woody vines like greenbrier (*Smilax spp*) and summer grape (*Vitis aestivalis*) (FNAI 2010).

Once prevalent throughout the southeastern U.S. coastal plain, the pine sandhill ecosystem has experienced a 98 percent decline in acreage throughout its range. It is now considered critically endangered (FNAI 2010). It is crucial to learn how to conserve and protect the composition and overall health of these ecologically important and sensitive areas. This type of conservative research is integral in land management of conservation areas, parks, state and private owned areas, where many times funding is limited and must be put to best use.

Optimal fire-frequency for prescribed burns within pine sandhill communities: an ongoing debate

The role of fire in maintaining sandhill and other pyrogenic communities in the southeastern United States has been recognized for more than a century (Pinochet 1899, Andrews 1917). In the 1940's (Platt et al. 1988; Hartnett and Krofta 1989; Boyer 1990; Myers 1990; Fowler and Konopik 2007) prescribed fire came to light as an integral part

of land management of communities dominated by pine (*Pinus palustris*) in Southeastern United States in order to maintain their unique species composition and structure (Ford et al. 2010). Since that time, substantial interest has been paid to the effect of differing fire return intervals, season of fire and fire behavior and intensity have on these communities (Ford et al. 2010). The issue of optimal fire frequency within pine communities has been the topic of heated debate among scientists and land managers alike.

The first contender in this debate is the Intermediate Disturbance Hypothesis (IDH), which is said to be one of the most often suggested non-equilibrium explanations for maintenance of species diversity (Wilson 1990). The second is the Most Frequent Fire Hypothesis (MFFH) (Glitzenstein et al 1996). Disturbance is the central issue at hand. The most common theme of disturbance is destruction of biomass which leads to an opening of space and utilization of resources by new individuals (Grime et al. 1987). The MFFH obviously is concerned with fire as the central disturbance, while the IDH is not always centered around fire.

The concept of the IDH can be traced to the 1950's when Hutchinson (1953) wrote of "a mechanism of coexistence in which catastrophic events created empty patches." The idea is that before a species had time to eliminate its weaker competitors, an empty patch opened in close proximity, leading to a "mixed population." Connell (1978) named this concept the "Intermediate Disturbance Hypothesis." There are four essential elements of the IDH:

- Repeated local disturbance which creates open (or partially open) patches;
- Disturbance frequent enough that competitive exclusion does not occur over the whole area, but not so frequent that most species are removed;

- Frequency of disturbance is seen in the context of generation time;
- A trade-off is assumed between species' colonizing ability and competitive ability (i.e. distinct colonist and climax species) (Wilson 1994).

An overarching issue with the IDH is the question “what constitutes a mechanism of coexistence?” The term has been used in a variety of ways in the literature, particularly in relation to how coexistence reacts to fluctuating environmental conditions (Roxburgh 2004). Some scientists (Sheil and Burslem 2003) posit that coexistence in “within-patch” and “between-patch” models constitute two different coexistence-promoting mechanisms (Roxburg 2004). These types of models depend on the relative sizes of the disturbance patch and the sampling area. In the within-patch interpretation, the sampling area is small in relation to the disturbance patch. An example of this type of mechanism would be that patches of mid-age are more species rich. In the between-patch mechanism, the sampling area is large in relation to the disturbance patches; therefore this type of mechanism would include patch disturbances of different ages, as some will be in early stages of colonization, some in mid stages and some at equilibrium (Wilson 1994).

While the IDH may seem intuitively simple, it is deceptively so (Roxburgh 2004). It has been said these concepts are an “elegant but over simplified representation of a complex knot of concepts” (Sheil & Burslem 2003). It may be easy to say that intermediate disturbance creates more richness or species coexistence, but in reality there may be many other underlying mechanisms contributing to the richness or coexistence of species in an area. It is also important for the researcher to describe “intermediate” and

“disturbance” when using the IDH, as the definition of these terms may change depending on the type of community and disturbance that is of interest.

A stark opponent of the IDH is the Most Frequent Fire Hypothesis (MFFH). In contrast to the IDH, which is broad in its definition of disturbance and type of habitat, the MFFH focuses directly on fire as the disturbance and pine sandhill as the habitat. This hypothesis suggests that the best management strategy for maintaining species richness and composition of native longleaf sandhill is to burn as frequently as fuels allow (Glitzenstein et al. 2003).

It is well known that a long-time lack of fire in sandhill communities allows hardwood species to close upper canopies, shading out longleaf pines and sandhill grasses, along with other pyrogenic species which require open canopy (Schmidt 2005). Jeff Glitzenstein et al. (1995, 2003) believe that low intensity fire is an important component of the natural disturbance regime among longleaf pine (*Pinus palustris*) dominated woodlands and savannas as this type of regime removes litter and keeps other non-fire adapted plants at bay.

If leaf litter is not frequently removed and builds up, it could lead to a hotter and longer burn, which could damage the cambium of trees and kill the root systems of even fire resistant shrubs & grasses. Another problem with large amounts of shrub and leaf litter in an area is that the fire can jump into the mid-canopy. A mid-canopy fire can lead to a major canopy fire, causing even old “tough” trees to die (Ford et al. 2010).

Meyers (1990), another proponent of the MFFH, reported that frequent low intensity ground fires during the growing season facilitate pine and wiregrass reproduction while reducing competition with hardwoods. He also found that the amount

of woody understory species increased with increased time between fires. Without relatively frequent fires, trees such as water oak (*Quercus nigra*), live oak (*Quercus virginiana*), sweetgum (*Liquidambar styraciflua*), common persimmon, laurel oak and other fast growing, fire sensitive trees invade and shade out the diverse ground layer (FNAI 2010).

Ecologists who disagree with the MFFH argue that very frequent burning may decrease productivity of pines and subsequently affect the community as a whole, yielding “unintended structural and functional consequences” (Ford et al. 2010). Although they are fire adapted, it is still possible to harm or kill a pine by exposing it to repeated fires in short succession (Ford et al. 2010) Ford et al. suggests that a dynamic burn schedule, such as initially burning at 1- and 2- year intervals followed by longer, more variable fire-return intervals may be beneficial.

A reason for this ongoing debate on optimal fire frequency in pine communities is the multitude of studies with mixed results in a variety of ecosystems. Some studies have found species richness to rise with fire frequency (Tester 1989; Mehlman 1992; Nuzzo et al. 1996). Other studies have found that increasing fire frequency leads to a decrease in species richness (Collins et al. 1995). Some have concluded that there is lowest richness at intermediately disturbed areas. In fact, Schwilk et al. found that species richness within the shrubland studied was highest at the least frequently burned sites (40 years between fires) and lowest at the sites of moderate (15 to 26 years between fires) and high fire frequency (alternating four and six year fire cycle).

There are many reasons for the inconsistency seen in the outcomes of these studies. One reason may be the fact that different studies had different times since last

fire. Another cause could be inclusion of dormant season burn, which may affect flora differently than growing season fires (Platt et al. 1993; Streng et al. 1993; Sparks et al. 1998; Beckage et al. 2000). Still another cause of inconsistency is that richness as a concept is meaningless without considering spatial scale. Much of the IDH research deals with within-patch and between-patch dynamics as aforementioned, while spatial scale is not considered in Glitzenstein's work on MFFH.

Beckage (2000) studied the effect of burning frequency on density and species richness of understory flowering stems in a Florida sandhill and tested it against the Intermediate Disturbance Hypothesis. He examined 12 papers that addressed the relationship between species richness and fire and found that each study generally suffered from "power problems" which unsurprisingly could lead to inconsistent results. After reviewing his results, he considered the possibility that his and other studies had low statistical power, resulting from a relatively small sample size. These inconsistent results suggest an overall need for a meta-analysis among the fire literature and more research, preferably with larger sample sizes (Beckage 2000).

Past and future research on pine sandhill

Research on pine sandhill communities in the past has, for the most part, focused on tree and canopy dynamics. Less is known about the understory of these communities, including richness, abundance, composition and successional progression of response after disturbance. A disturbance such as fire affects the community system as a whole, yet it is also important to break apart the components of the community to examine other factors that may be at play in the system such as elevation, soil type, past disturbance, or

spatial scale. It is imperative to acknowledge these factors when assessing and planning a burn strategy. This research may be the first of its kind to use species area curves and relationships to focus on richness of a pine sandhill community.

Species area curves: a quick background

A key pattern in ecology, in which the number of species increases as area increases, has been recognized since the 1850s, first by de Candolle in 1855. This pattern can be illustrated in the species area curve, which was formalized in 1921 by Arrhenius (followed by Gleason 1922, Cain 1958, McIntosh 1985). The species area relationship has two basic causes, the first being that as more individuals are sampled, the chance of coming across additional species grows. The second cause is that a larger area is more likely to be environmentally heterogeneous, containing additional species which differ in their niches (Scheiner 2003).

An advantage of the species area curve is its flexibility and functionality. There is a variety of species area curves, which differ in both the way data are collected and in the way the curve is constructed. Scheiner (2003) defines six ways to estimate species area curves. There are 4 types of sampling, as shown in Figure 1, and 2 ways of calculating Type II and Type III curves.

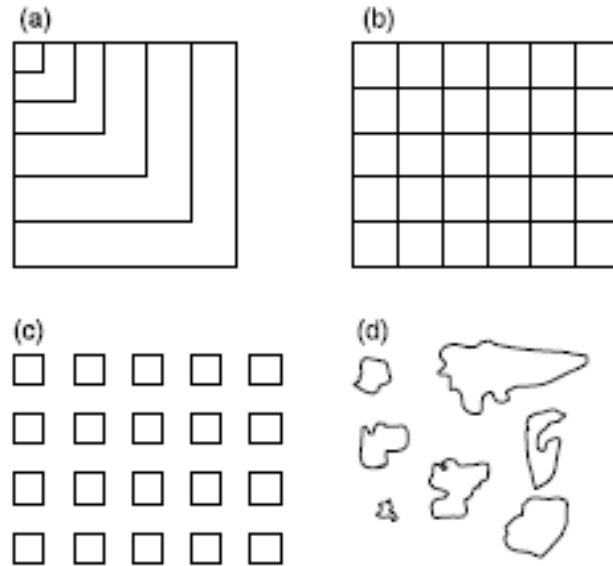


Figure 1. Four general sampling schemes of species area curves. (a) strictly nested quadrats (Type I curves); (b) quadrats arrayed in a contiguous grid (Type II curves); (c) quadrats arrayed in a regular but noncontiguous grid (Type III curves); (d) areas of varying size, often islands (Type IV curves) (Scheiner 2003).

Each data point is based on a single measurement for a given size for a Type I or Type IV curve. Type II and Type III curves are constructed by estimating the mean diversity for a given area, which can be done in two ways: spatially explicit or spatially non-explicit.

Spatially explicit methods retain information on the spatial arrangement of quadrats (Type IIA and Type IIIA curves) while the alternative is to ignore spatial information (Type IIB and Type IIIB). There are two ways to create curves from data gathered from a non-contiguous grid, Type IIIA and IIIB. The spatially explicit method, or Type IIIA, begins by calculating the mean diversity for each quadrat, providing the first data point – the mean number of species in an area of 1 unit. Next, determine the diversity of all combinations of adjacent quadrats and again calculate the mean – the mean number of species in an area of 2 units. Do this again for triplets, quadruplets and

so forth. For Type IIIA curves, use the nearest quadrats rather than adjacent ones. Ignore spatial arrangement. Again begin with single quadrats and go on to pairs, triplets and so forth. But now, all possible pairs, triplets or quadruplets are used, not only adjacent quadrats. (Scheiner 2003).

Debate on the best mathematical function for the species area curve

The relationship between the number of species and area can be described by many different functions, and how well they fit the data may vary among different systems and sampling schemes (Scheiner 2000). Historically, there has been debate on what the best mathematical function for the shape of the species area curve ought to be (He & Legendre, 1996; Tjørve, 2003), (Scheiner 2003). Scheiner et al. (2011) noted over 27 different functions, most attention has been given to three of them:

the exponential curve (Gleason, 1922, 1925),

$$S = z \ln(A) + c$$

the logistic curve (Archibald, 1949),

$$S = b/(c + A^{-z})$$

and the power curve (Arrhenius, 1921, 1923a,b),

$$\ln(S) = z \ln(A) + c$$

where S is the number of species, A is the area, and b , c and z are constants (Scheiner 2003).

Spatial scale of sampling must be considered when choosing a species area model as the species area relation takes on different forms depending on it (He et al. 1996). At a

very local scale, accumulation of new species is relatively slow within an area due to the probability of strong similarity of environmental conditions and species composition of neighboring areas (He et al. 1996). The exponential model, once widely accepted by ecologists but now mostly ignored, is more suited under these conditions (He et al. 1996). It can only be applied within limited regions, as unbounded growth of species number is clearly not realistic. Although species number may initially grow exponentially, in any study area, there will eventually be no new species (Meadows 1972).

As the spatial scale increases, heterogeneity increases as soon as we surpass the effective range of the spatial autocorrelation of the environmental conditions. In this case, the number of new species accumulates at a faster rate and can best be described by the power curve (He et al. 1996). It is widely held that the power function is the best model based on Preston's (1962) derivation of a power function from a lognormal species abundance distribution (Scheiner et al. 2011). He et al. (1996) suggest that the reason the power model is most widely used is that most field sampling programs are not large enough to use the logistic curve.

As sampling area continues to increase, acquisition of new habitats slows down and finally ceases while the rate at which new species are encountered is reduced until a different type of community is encountered (He et al. 1996). If sampling covers the entire community, logistic can be expected to be the best model (He et al. 1996), but if the sample size is small, the test has low power and is unable to detect subtle deviations (Nemes 2009).

The decision to select a model ultimately must rest on data in most cases. The procedure to select the best model should include fitting several models to the real data

and comparing the results using statistical criteria (Conner and McCoy 1979). For any particular data set, there exists a best model but there is no model that is universally best (He et al. 1996)

The role of scale in species area curves

To fully understand species area curves, one must take into account the components of scale used to create them: sampling unit, grain, focus and extent. When studying species area curves, these components are very important as richness is not entirely useful without taking into account scale. For example, imagine you are told that there are 10 different species of fish in a pond. Isn't it more informative if you know that pond is 0.25 hectares versus 25 hectares? Scheiner gives the following definitions for these components of scale. Sampling unit is the spatial and/or temporal dimension of the collection unit. Grain is the dimension to which data are standardized before analysis, often equal to the area, volume, or duration of the sampling unit. Focus is the dimension of the aggregated or summed grains. Extent is the coarsest spatial or temporal dimension that encompasses all of the sampling units (Scheiner 2011).

Type A curves estimate the rate of change of mean α -diversity (the mean number of species/m²) as grain increases (Tuomisto 2010b). Type B curves estimate γ -diversity (the total number of species in the cumulative 1-m² quadrats) and its rate of change as the focus increases (Scheiner et al. 2010). If Type IIIA and Type IIIB curves are different from one another, this indicates intraspecific spatial aggregation of individuals (Chiarucci et al. 2009). In this study, Type IIIB species area curves were constructed.

How species area curves can be used to examine plant species richness in pine sandhill

Species area curves can be used to understand a variety of ecological processes including island biogeography (understanding the number of species that an island can support), to estimate species extinction risk due to habitat loss or describing species diversity patterns following a disturbance (Scheiner et al. 2011). Species area curves can be used for conservation purposes to investigate how fragmentation may reduce the number of species supported by a particular habitat (Hill & Curran 2001). They can also be used to standardize estimates of inventory richness across different sites or times, an important tool when meta-analyses are being utilized to incorporate different data sets or studies (Scheiner et al. 2011). Species area curves can also be used to indicate heterogeneity in a community, but cannot pin-point or distinguish among mechanisms, as heterogeneity may be the result of many different factors (Scheiner et al. 2011). Therefore, it is prudent to expand research once heterogeneity has been found using species area curves in order to attempt to find the source or sources. We examined soil, elevation, and burn regime as explicit sources of heterogeneity. We also examined the spatial scale of heterogeneity.

Spatial autocorrelation and the relationship between species composition and abiotic factors

Most environmental data are autocorrelated (Legendre 1989). There are legitimate reasons for autocorrelation. The goal is to recognize its existence and account for it in the model. A Durbin-Watson test can be performed to test for autocorrelation among residuals. While it can say if the residuals of a system are autocorrelated, it cannot tell us

what is actually causing the autocorrelation. The Durbin-Watson test is useful in that it can examine heterogeneity on different spatial scales.

One may also wish to study the relationship between species composition and certain abiotic factors such as geographic distance, elevation or burn regime. The Mantel test can do this by measuring the correlation between two matrices, for example one containing spatial distances and one containing species dissimilarity. Mantel correlograms can be used to provide a description of the spatial structure by looking at their shape, which can provide information about underlying generating processes. (Legendre 1989).

Objectives and what we hope to accomplish

We studied a pine sandhill community in Southern Florida. The study took place in the partitioned burn plots of the University of South Florida's Ecological Research Area in Tampa, Florida and had multiple objectives. The first was to describe species richness in the sandhill. Next was to examine similarity among burn plots. We also determined if autocorrelation of the residuals was at play in this system. We examined heterogeneity and its causes in this site. We used our results to challenge the two most prevalent theories of best fire regime in these communities and also to explore patchiness and compositional patterns in this system.

These results can contribute to the ongoing debate on the optimal fire-frequency for prescribed burns within pine sandhill communities and in best management practices for conservation of these areas. It is vital to continue researching these integral habitats and remain focused on what can be done to conserve them for future generations.

METHODS

Study site

This study took place in the University of South Florida's Ecological Research Area (ERA) in Tampa, Florida (27°57'N, 82°32'W), a 200 ha swath of a land which borders the Hillsborough River. This area has a humid subtropical climate with mild winter temperatures (long-term mean 17.5 °C) and hot summer temperatures (long-term mean 27.3 °C). In 1976, an expanse of sandhill community within the ERA was divided into 10 plots of approximately 1 ha. A prescribed fire-return interval of 1, 2, 5 or 7 year or unburned treatment plots was randomly assigned (n = 2 replicates, east and west) to each plot. All prescribed fire treatments occurred during mid-May through early August. For the most part, burns occurred as scheduled but during some years for various reasons, no burns took place (e.g. 1993, 1995 and 1997). The 1- and 2- year fire interval treatments were mainly affected by these non-fire events, resulting in actual mean intervals of 1.5 and 3 years. Due to these irregularities, the 1- and 2- year treatments should be thought of as “more frequent” and 5- to 7- year treatments as “less frequent” fire-return intervals. (Ford et al. 2010).

Data collection

I generated a map of the Ecological Research Area's burn plots in ArcGIS using ArcMap (Digital Orthophoto SWFWMD 2009) and created a regular grid with points

every 30m to identify sampling locations. This established a total of 136 1m X 1m sampling quadrats (each centered on a grid point) as shown in Figure 2. Figure 3 illustrates quadrat and transect spacing. Because the burn plots are not of equal size, the regular grid means that some plots were sampled more than others. I recorded longitudinal and latitudinal coordinates of each quadrat from this grid. I utilized a handheld GPS (Garmin eTrex Legend) to pinpoint the location of each quadrat within the study area to at least 3 m in accuracy and staked each quadrat so it could be revisited in the future.

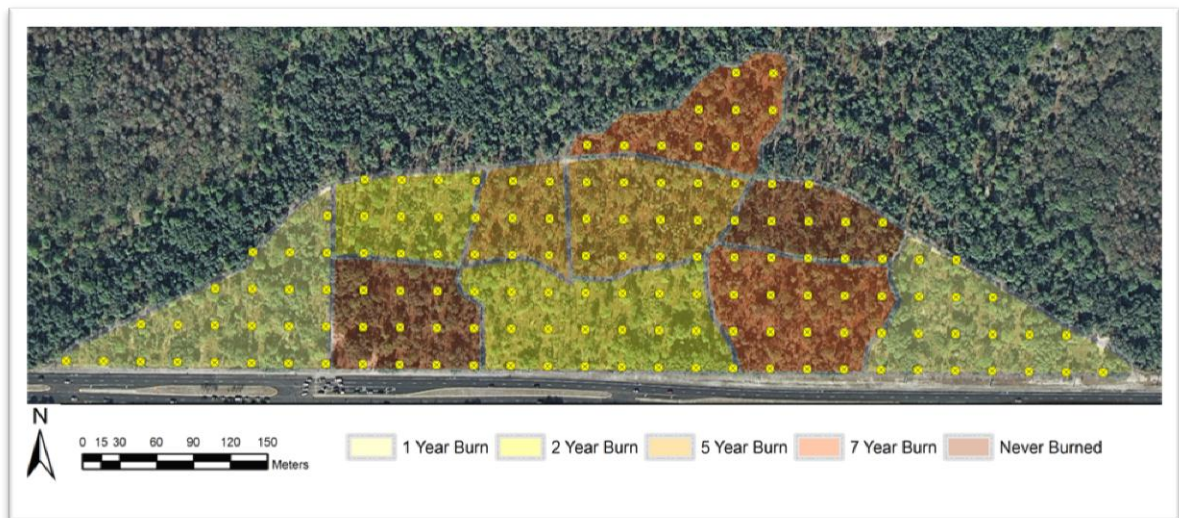


Figure 2. GIS map of burn plots within the University of South Florida Ecological Research Area [ERA]. Each color grade represents a different burn regime, of which there are 2 replicates of each.

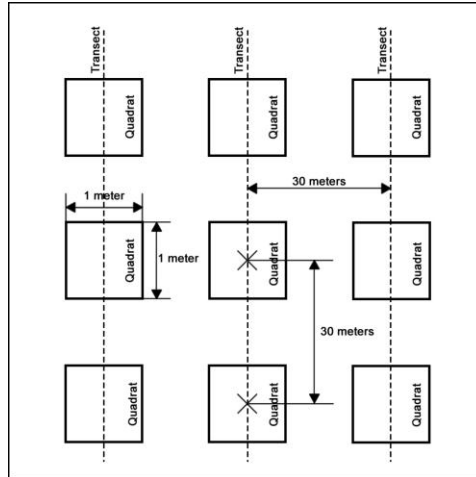


Figure 3. Illustration of quadrat & transect spacing. Each quadrat is 30m apart and staked in the center.

I collected counts of species richness in two surveys, one occurring in the Spring of 2009 and the following survey during the Fall of 2009. I recorded careful visual observations of plant species richness at each quadrat. These observations encompassed all plants, including herbaceous plants, shrubs and trees. I collected and preserved any unknown species.. Identification methods included conventional identification keys, field guides, expert consultation, and comparison with catalogued species at the USF's Institute for Systematic Biology Herbarium. 11 specimens remain unidentified due to lack of testable material or degradation of the sample. .

Data analysis

We analyzed data using R, a statistical computing and graphics program (R Development Core Team (2010). This R code is available upon request. From a library in R called “vegan”, we found initial descriptive information such as total number of distinct species, maximum and minimum richness of observation points, and mean

richness. To show how often each species was found in the survey, we produced a curve of rank occurrences.

We generated empirical species area curves and upon visual examination, we chose the power, not logistic or exponential, for our data. While the empirical data do not have the exact characteristics of any of these models, they are more like the power curve than the logistic or exponential. Therefore we focused on asking questions about the power curve and departures from it. To do this, we fit the pooled curve to a linear log-log model. Non-linearity is caused by heterogeneity within the sampled system. It follows to ask “what is causing heterogeneity in this system?” This is not an easy question to answer and is not readily apparent. However, a logical first step towards better understanding the system is to examine the scale of heterogeneity. We fit curves individually for each burn plot and asked whether these more closely approached linearity – that is, is much of the heterogeneity between the burn plots? These individual curves were also fit to a linear log-log model. To examine differences between these fits, we constructed analysis of variance tables. We looked for non-linearity in curves both graphically and using a Durbin-Watson test of the autocorrelation of the residuals.

To examine compositional similarity among burn plots, we ran a simple Jaccard dissimilarity estimate for all pairs of burn plots. To test whether physically closer samples are more compositionally similar than farther apart samples, we used a simple Mantel test. The Mantel test does this by measuring the correlation between the Jaccard dissimilarity matrix and a physical distance matrix. We also used a simple Mantel test to examine whether similarly burned sites have similar species compositions. This can be done in two ways. The first is to substitute 35 years for the unburned treatment, which is

the minimum time since fire for the unburned plots. The second way is to treat every distance as either 0 or 1. Zero represents two quadrats in the same burn treatment and one represents two quadrats of different treatments.

In order to investigate the relationship between Jaccard dissimilarity and physical distance while controlling for the effects of burn treatment, we created a pair of Mantel correlograms. We produced another pair of Mantel correlograms which examined the relationship between Jaccard dissimilarity and physical distance while controlling for the effects of elevation.

We used an elevation data shape layer (Digital Orthophoto SWFWMD 2009), which was overlaid on the map of the Ecological Research Area's burn plots in ArcMap, to estimate elevations of each burn plot. We then examined correlations of species richness and elevation.

We implemented a soils shape layer but it was shown that the soils were similar throughout, except for a small patch in the upper western area of the burn plot area. This area was not large enough to have an appreciable effect in the results.

RESULTS

Species occurrence and distribution of richness

A total of 85 species were identified within the sample. The three most prevalent species observed were *Aristida stricta* (Wiregrass), *Dichanthelium portoricense* (Hemlock witchgrass), *Quercus geminata* (Sand live oak) (N=93, N=53, and N=49; respectively).

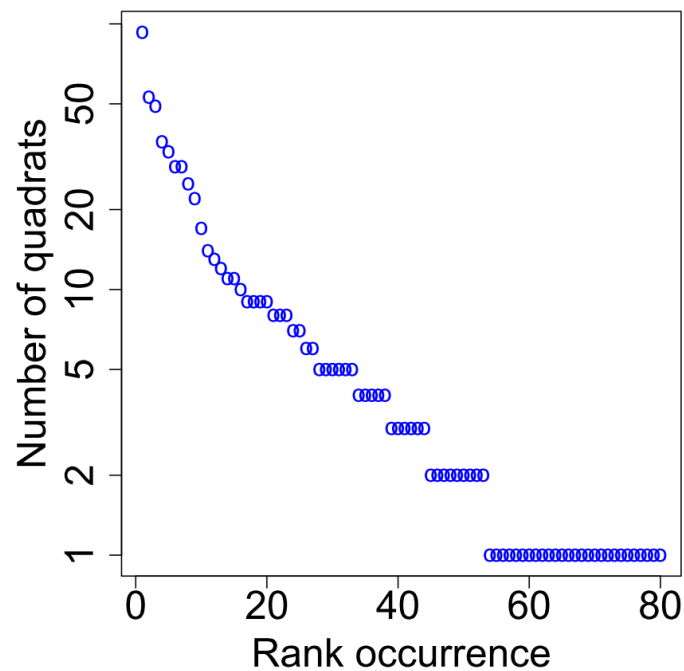


Figure 4. Rank species occurrence over study area. Each circle represents a unique species.

There were 27 species that occur in only one quadrat and nine species which occur in two quadrats (Figure 4). Of the 27 species that occurred once, nine were unidentifiable due to a lack of testable material. A previous collection made in the study area by Anne Schmidt (2005) listed nine of the species found only once as occasional (taxa found sporadically throughout), four as rare (taxa with one to very few individuals

throughout) one as frequent (taxa easily found throughout). Four species were not listed in Schmidt's study. Of those four species, *Setaria pumila* is considered a noxious weed (Plant 2010). *Trifolium repens* can be considered a weedy exotic species (Wunderlin & Hansen 2008). *Smilax tamniodes* and *Viola primulifolia* are native to Florida and not of special concern (Wunderlin & Hansen 2008).

The distribution of richness per quadrat (Figure 5) is positively skewed. The maximum richness of any quadrat was 11 species. The minimum richness was zero species, which was only encountered once. Most of the quadrats contain 3-5 species. Sixteen quadrats contain 1 or 2 species, and only 5 quadrats have more than 8 species within them. The mean richness throughout was 4.8 species per quadrat.

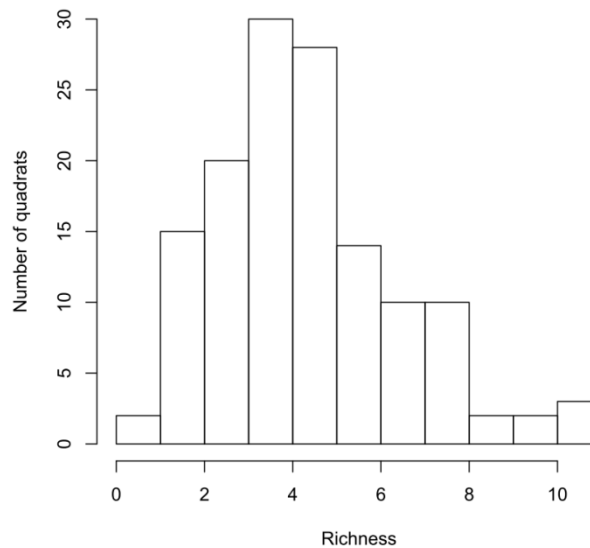


Figure 5. Distribution of richness per quadrat. Median richness per quadrat is 4 species and the mean is slightly higher at 4.8 species.

Linearity of the species area curves and similarity of richness among burn plots

The species area curve pooled across all plots (Figure 6) is significantly non-linear compared to the best fit line. In fact, the observed empirical curve crosses the best fit line in two places. The intercept of the empirical curve is lower than the best fit line, while the slope of the empirical curve is higher than the best fit line. The error bars for the empirical curve at all times overlap the best fit line.

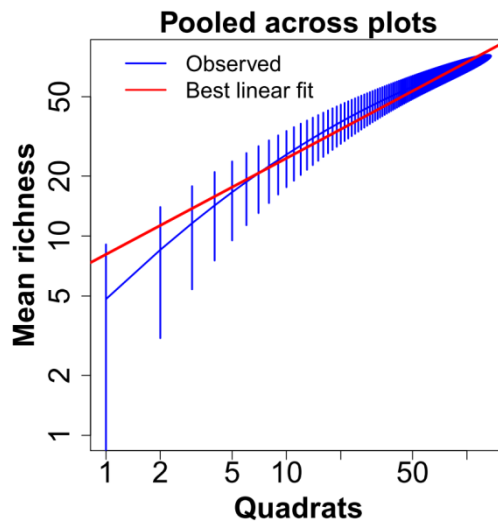


Figure 6. Species area curve based on species richness calculated from all possible combinations of quadrats. The best fitting linear model is shown for comparison.

. The linear fits to the individual plot data appear to be much closer to linear than the pooled data (Figures 6 and 7). Although departures from linearity are small in each plot, there is an additive effect caused by variation among the individual burn plots which leads to the overall larger departure from linearity seen in the pooled data.

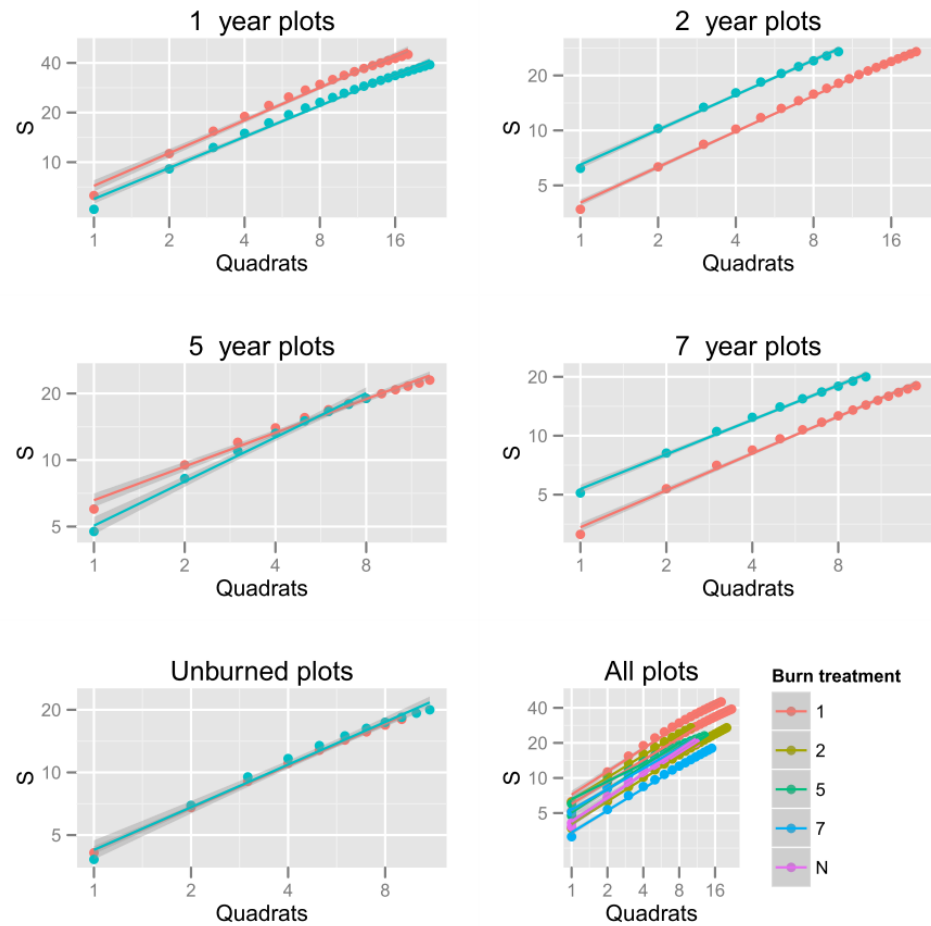


Figure 7. Species area curves for all each burn treatment. Replicate burn treatments often have different slopes and intercepts. See Figure 8.

The heterogeneity of slopes model confirmed that individual plots are different from one another regardless of whether they have the same burn regime. The differences are not always great; therefore, it is useful to examine the slopes and intercepts of each plot (Table 1, Figure 8).

Table 1. Slopes and intercepts for all linear fits. 2W exhibits the highest intercept, while NE exhibits the steepest slope.

	Intercepts	Slopes
1E	0.73	0.68
1W	0.71	0.68
2E	0.60	0.67
2W	0.76	0.63
5E	0.75	0.53
5W	0.66	0.68
7E	0.63	0.66
7W	0.72	0.57
NE	0.60	0.70
NW	0.63	0.68

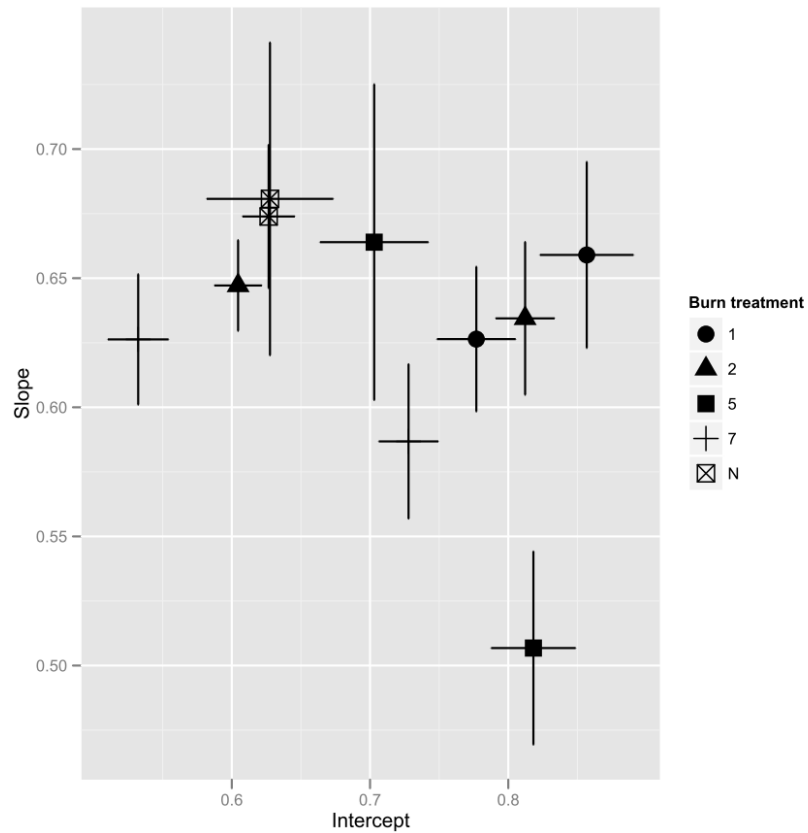


Figure 8. Illustration of intercepts and slopes of the best fit linear regressions for richness. With the exception of 5E and 7W, the slopes are similar throughout while the intercepts vary.

The slope is quite similar throughout all plots except 5E and 7W, while the intercept varies considerably more (Figure 8). The largest difference in slope within a burn regime was the 5 year regime. The largest difference in intercept within a burn regime was the 2 year regime. The smallest difference in both slope and intercept within a burn regime was the 1 year regime. 2W had the highest intercept (0.76) while NE had the highest slope (0.70). 5E had the smallest slope (0.57) while NE had the smallest intercept (0.60). 1E, 1W, 5W and NW all shared the same slope (0.68).

The results of the Durbin-Watson test confirm that the residuals are autocorrelated, as all of the fits failed. Plot 1E (Figure 9) exhibited the highest departure from linearity of the best fit line. The residuals are autocorrelated in all plots (showing that the data are not strictly linear) but the departures from the lines are fairly small.

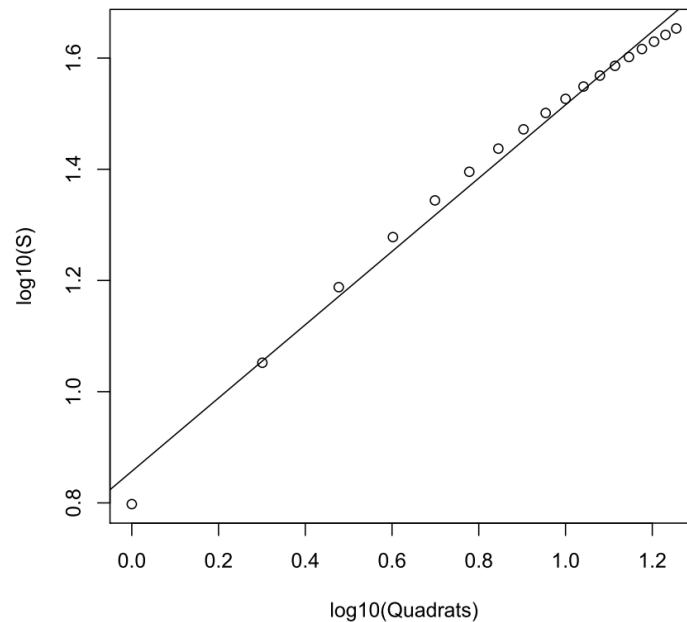


Figure 9. Best fitting linear model for plot 1E (Durbin-Watson). Plot 1E exhibited the largest autocorrelation among residuals.

Jaccard dissimilarity and the effects of physical distance, burn regime and elevation on compositional similarity among burn plots

There was no clear pattern of dissimilarity. Plots 1W and 2W were the most compositionally similar, while 2E and 7E were the most dissimilar. Overall, the compositional similarity in this system did not have much of a relationship with burn regime.

The null hypothesis that the two matrices, Jaccard dissimilarity and physical distance, are unrelated was rejected (Mantel $r=0.15$, $p\text{-value}=0.002$, 95% confidence interval) suggesting that the matrix entries are positively associated. Smaller differences in species composition are generally seen among pairs of quadrats that are closer to each other than far from each other. A significant association was also found between the Jaccard dissimilarity and burn treatment (Mantel $r=0.014$, $p\text{-value}=0.347$, 95% confidence interval). Therefore, the relationship between similarity and physical distance appears to be stronger than that between similarity and burn treatment.

When the effects for burn treatment were removed, the correlogram did not change appreciably (Figures 10 and 11). This indicates that burn treatment does not have a significant effect on compositional similarity. Equally, when the effects for elevation were removed, the correlogram did not change appreciably. This indicates that elevation does not have a great effect on compositional similarity.

The correlograms exhibited a positive correlation which declined as distance increased. There ceased to be any correlation after around 200m, which is similar to the size of a burn plot. Again we see physical distance, not burn treatment, may be the most significant factor at play in this system.

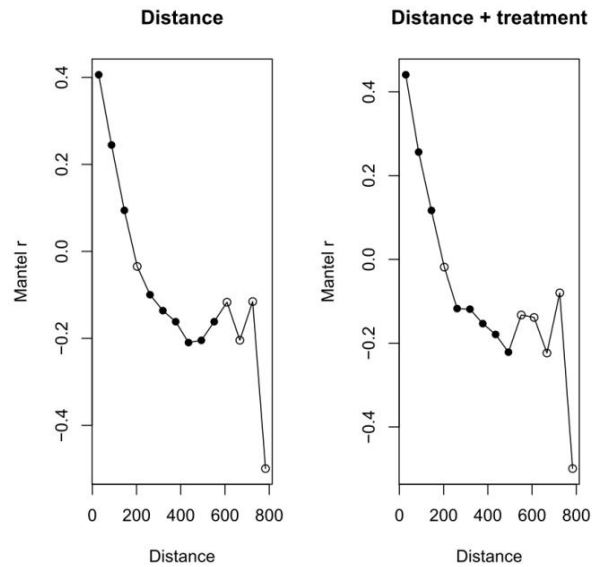


Figure 10. Mantel correlograms for Jaccard dissimilarity vs. distance alone (left) and Jaccard dissimilarity vs. distance, holding treatment constant (right). Unfilled circles are non-significant. Burn treatment does not have an appreciable effect on compositional similarity.

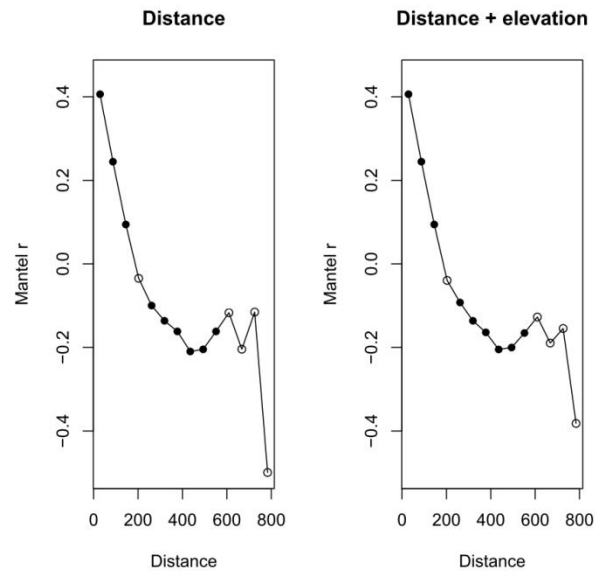


Figure 11. Mantel correlograms for Jaccard dissimilarity vs. distance alone (left) and Jaccard dissimilarity vs. distance, holding elevational difference constant (right). Unfilled circles are non-significant. The effects of elevational difference on compositional similarity are minimal.

Effect of elevation on species richness within burn plots

Richness seemed to vary unpredictably by elevation (Figure 12). The one year plots had the largest range of elevation and the richness in these burn plots declined with elevational rise. The 7 year plots have two different elevations but the richness is somewhat similar. In some burn regimes, richness may rise with elevation in one plot and fall with elevation in the other. Overall, no relationship between richness and elevation was could be garnered from this graph.

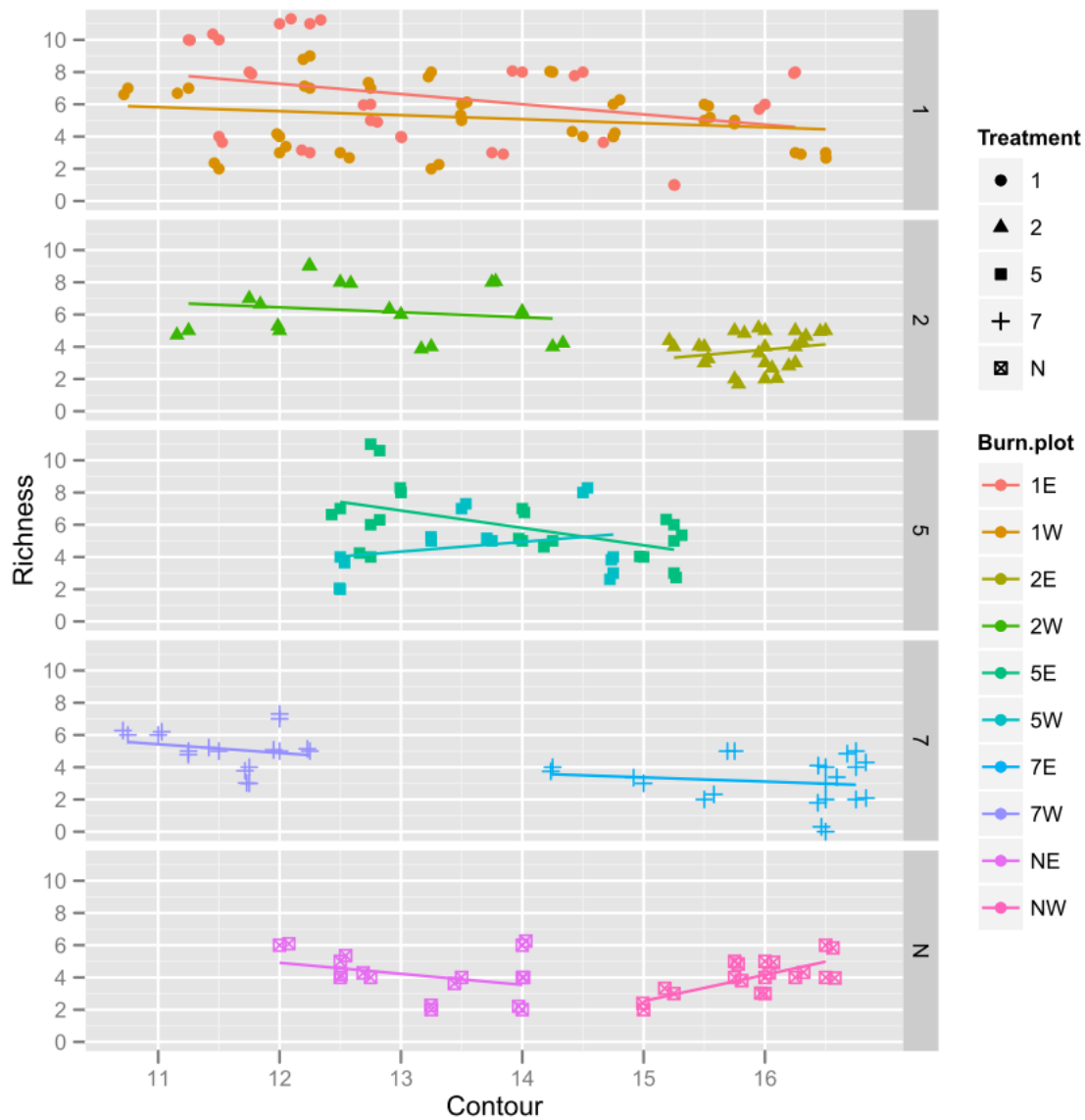


Figure 12. Species richness in each burn plot, as a function of elevation contour. No single pattern can be discerned. Richness changes with elevation differently in different burn plots.

DISCUSSION

Species occurrence and distribution of richness

The species occurrence curve gave a good impression of the overall composition and species distribution of the study area. A small number of dominant species covered large amounts of area while many occasional or rare species were interspersed throughout. The results of the occurrence curve were compared to a previous collection within the study area by Anne Schmidt in 2005. The occurrences were commiserate. Frequently found species in this study were also frequently found in Schmidt's study, and so on. The total number of species found in this study was 57% of the total number of species found in Schmidt's previous study.

The results of the distribution of richness per quadrat figure gave an impression of the patchiness of the study area. In any 1mx1m area, one may expect to find an average of 4.8 species. It was rare to encounter a 1mx1m area with no species or a 1mx1m area with more than eight.

Linearity of the species area curves and similarity of richness among burn plots

The pooled species area curve exhibited a significant departure from linearity caused by the additive effects of the individual burn plots' departures from linearity. A departure from linearity suggests heterogeneity within the environment. The individual burn plot species area curves were closer to linear than the pooled curve. The individual plots can be said to have less environmental heterogeneity but when all plots were summed together, the additive effect of heterogeneity created the pooled curve with a

larger departure from linearity. As the study area increases, the chance of encroaching upon areas that are environmentally heterogeneous with additional species which differ in their niches rises. As such, it was not surprising to see the larger departure from linearity in the pooled data. While heterogeneity was detected, the cause or causes of environmental heterogeneity cannot be predicted using only species area curves.

We examined the similarity of the intercepts and slopes of the individual burn plots, which represent initial species richness and species acquisition rate respectively. For the most part, the slopes were quite similar throughout burn plots. The least different burn regime in both slope and intercept was the one year regime, which meant that both one year burn plots initially had the same number of species, and were acquiring species at the same rate. The second most similar burn regime was the unburned plots. The most different burn regime was the five year plots. 1E, 1W, 5W and NW had the same slope, which meant that they were all acquiring species at the same rate. There was not a significant difference in the species acquisition rate between burn plots of differing regimes. On this scale, these results support neither the Intermediate Disturbance Hypothesis nor the Most Frequent Fire Hypothesis. From this we concluded that although integral to the survival of the community, burn regime was not the most important or only contributing factor controlling for richness in this system. Neither intermediate burning nor very frequent burning seemed to significantly increase or obviously affect species richness.

The Durbin-Watson test confirmed that the species area curves were not linear but curved, as seen in the pooled species area curve and individual plot curves. Plot IE exhibited the highest autocorrelation among the residuals, but even this autocorrelation

was fairly small. Although there was departure from linearity, it was not so much that we worried about the integrity of our sampling or sampling design. There are legitimate reasons for autocorrelation and it is to be expected in any natural system.

Jaccard dissimilarity and the effects of physical distance, burn regime and elevation on compositional similarity among burn plots

We could not draw any concrete conclusions from the results of the Jaccard dissimilarity test as there was no clear pattern of dissimilarity among plots. We implemented a more sophisticated set of tests, Mantel tests and Mantel correlograms, in order to delve deeper into the question of compositional dissimilarity of the burn plots and what may be causing heterogeneity seen in the study site.

We rejected the null hypothesis of the Mantel test that the Jaccard dissimilarity and distance matrices were unrelated (Mantel $r=0.15$), which meant that physically close samples were more compositionally similar than farther apart samples. In other words, there were smaller differences in species composition among samples that were closer together.

We also rejected the null hypothesis of the Mantel test that the Jaccard dissimilarity and burn treatment matrices were unrelated (Mantel $r=0.014$). This confirmed a correlation between compositional dissimilarity and burn treatment and that there were smaller differences in species composition among samples that were similarly burned. A Mantel r of 0 represents no relation of the matrices, consequently the correlation was quite weak. Overall, the results of the Mantel tests revealed that the relationship between compositional dissimilarity and physical distance was stronger than the relationship between compositional dissimilarity and burn treatment.

To further test the hypothesis that physical distance had more of an affect on compositional dissimilarity than burn treatment, we created Mantel correlograms, which are recalculations of the Mantel correlations for samples at difference distances. The first set of correlograms examined the relationship between Jaccard dissimilarity and physical distance while controlling for the effects of burn treatment. When the effects for burn treatment were removed, the correlogram did not change appreciably. This suggested that burn treatment did not contribute much to species compositional dissimilarity within the sampling area.

The second set of Mantel correlograms examined the relationship between Jaccard dissimilarity and physical distance while controlling for the effects of elevation. When the effects for elevation were removed, the correlogram did not change appreciably. This suggested that elevation did not contribute much to species compositional dissimilarity within the sampling area.

The Mantel correlograms exhibited a positive correlation which declined as distance increased. At a distance of 200m, the correlation became negative. The average size of a burn plot within the study area was about 200m. The results of the Mantel correlograms seemed to support a “plot effect.” Species within one plot are more compositionally similar than species in any other plot. The results of the Mantel tests and correlograms were surprising to us. We expected to see similar species composition in plots of similar burn regime, but discovered that physical distance has more to do with compositional dissimilarity and burn treatment or elevation. This may be a result of seed dispersal limitations among species.

Lastly, we examined how species richness was affected by elevation. Elevation varied unpredictably among burn plots. For the most part, these species were shallow rooted, therefore elevation may not be very influential.

We concluded that although burn treatment and elevation must contribute to the environmental heterogeneity of this system in some ways, these factors did not act as we thought they would. These findings are important because it shows definitively that burn treatment was not the only or most important factor in maintaining the richness of this area.

Conclusions

We examined patterns of species richness in the burn plot area of the University of South Florida's Ecological Research Area (ERA) and how it changed with spatial scale. We also examined similarity of the burn plots in species composition and what the effects of burn treatment and elevation were on species compositional dissimilarity. We found no obvious patterns of similarity among burn plots of the same regime. We also found that environmental heterogeneity was occurring in the system but could not pinpoint exactly what was causing it. We looked at burn treatment and elevation and found that neither factor was contributing heavily to the observed environmental heterogeneity. This was surprising because we assumed that burn regime would be the main factor contributing to the species composition and species richness of the study area.

We discovered that the role of fire and other factors in these systems is much more complex than it may seem to be. We know that burning is essential in pine sandhill

communities but ecologists and land managers are still attempting to discover how to best preserve, conserve and restore these ecologically important and sensitive areas.

Our results suggest a need for a dynamic plan for the conservation, preservation and management of pine sandhill communities. One must consider as many factors as possible when managing these lands, as every sandhill is unique. We found that physical distance was important in the species compositional differences in one area versus another, but species richness and composition can be affected not only in space but also in time. This fact lends itself to the importance of studying the pine sandhill communities over a long period of time. Years of drought or plentiful rainfall may favor the establishment of some species over others. Similarly, short or long fire intervals may favor some species in subtle ways. It is obvious that more research must be done to fully understand pine sandhill communities.

Like a doctor acknowledges a patient's past and present health in order to diagnose and treat an illness, land managers and ecologists must observe each individual sandhill community and recognize its unique set of circumstances so as to create an appropriate strategy to maintain its unique species composition and structure.

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APPENDICES

Appendix A: Extra Tables

TABLE A1: Plant species identified¹

<u>Genus & Species</u>	<u>Family</u>	<u>Acronym</u>	<u>#</u>
<i>Ageratina jucunda</i> (Green) Clewell & Wooten)	Asteraceae	AGJU	5
<i>Aristida stricta</i> Michx.	Poaceae	ARST	93
<i>Ampelopsis arborea</i> (L.) Koehne	Vitaceae	AMAR	1
<i>Andropogon spp</i>	Poaceae	ANSP	1
<i>Andropogon ternarius</i> Michx.	Poaceae	ANTE	4
<i>Andropogon virginicus</i> L.	Poaceae	ANVI	6
<i>Balduina angustifolia</i> (Pursh) B.L.Rob.	Asteraceae	BAAN	11
<i>Berlandiera subacaulis</i> (Nutt.) Nutt.	Asteraceae	BESU	8
<i>Callicarpa americana</i> L.	Lamiaceae	CAAM	2
<i>Carphephorus corymbosus</i> (Nutt.) Torr. & A. Gray	Asteraceae	CACO	5
<i>Cenchrus gracillimus</i> Nash	Poaceae	CEGR	2
<i>Chrysopsis scabrella</i> Torr. & A. Gray	Asteraceae	CHSC	2
<i>Chrysopsis spp</i>	Asteraceae	CRSP	9
<i>Cnidoscolus stimulosus</i> (Michx.) Englem. & A. Gray	Euphorbiaceae	CNST	13
<i>Croton argyranthemus</i> (Michx.)	Euphorbiaceae	CRAR	2
<i>Croton michauxii</i> G.L. Webster	Euphorbiaceae	CRMI	2
<i>Cyperus retrorsus</i> Chapm.	Cyperaceae	CYRE	1
<i>Desmodium floridanum</i> Chapm.	Fabaceae	DEFL	1
<i>Dichanthelium aciculare</i> (Desv. Ex Poir.) Gould & C.A. Clark	Poaceae	DIAC	1
<i>Dichanthelium portoricense</i> (Desv. ex Ham.) B.F.Hansen & Wunderlin	Poaceae	DIPO	53
<i>Digitaria ciliaris</i> (Retz.) Koeler	Poaceae	DICI	1
<i>Diospyros virginiana</i> L.	Ebenaceae	DIVI	8
<i>Elephantopus elatus</i> Bertol.	Asteraceae	ELEL	8
<i>Eragrostis elliottii</i> S. Watson	Poaceae	EREL	12
<i>Eragrostis virginica</i> Salzm. ex Steud.	Poaceae	ERVI	2
<i>Eriogonum tomentosum</i> Michx.	Polygonaceae	ERTO	1
<i>Eupatorium capillifolium</i> (Lam.) Small	Asteraceae	EUCA	33

APPENDICES (CONTINUED)

<i>Eustachys neglecta</i> (Nash) Nash	Poaceae	EUNE	3
<i>Eustachys petraea</i> (Sw.) Desv.	Poaceae	EUPE	9
<i>Galactia regularis</i> (L.) Britton, Sterns & Poggenb	Fabaceae	GARE	25
<i>Galactia</i> spp	Fabaceae	GASP	3
<i>Galium hispidulum</i> Michx.	Rubiaceae	GAHI	1
<i>Helianthemum corymbosum</i> Michx.	Cistaceae	HECO	17
<i>Houstonia</i> spp	Rubiaceae	HOSP	5
<i>Lechea</i> spp	Cistaceae	LECSP	1
<i>Leucanthemum</i> spp	Asteraceae	LESP	4
<i>Liatris pauciflora</i> Pursh	Asteraceae	LIPA	1
<i>Liatris</i> spp 1	Asteraceae	LISP1	11
<i>Liatris</i> spp 2	Asteraceae	LISP2	9
<i>Liatris</i> spp 3	Asteraceae	LISP3	2
<i>Liatris</i> spp 4	Asteraceae	LISP4	3
<i>Lupinus villosus</i> Willd.	Fabaceae	LUVI	10
<i>Mimosa quadrivalvis</i> L.	Fabaceae	MIQU	4
<i>Opuntia humifusa</i> (Raf.) Raf.	Cactaceae	OPHU	2
<i>Palafoxia integrifolia</i> (Nutt.) Torr. & A.Gray	Asteraceae	PAIN	1
<i>Parthenocissus quinquefolia</i> (L.) Planch.	Vitaceae	PAQU	1
<i>Paspalum setaceum</i> Michx.	Poaceae	PACI	1
<i>Pinus palustris</i> Mill.	Pinaceae	PIPA	7
<i>Pityopsis graminifolia</i> (Michx.) Nutt.	Asteraceae	PIGR	36
<i>Polygala violacea</i> Aubl.	Polygalaceae	POVI	1
<i>Quercus geminata</i> Small	Fagaceae	QUGE	49
<i>Quercus incana</i> Bartram	Fagaceae	QUIN	5
<i>Quercus laevis</i> Walt.	Fagaceae	QULA	22
<i>Quercus virginiana</i> Mill.	Fagaceae	QUVI	1
<i>Rhynchosia reniformis</i> DC.	Fabaceae	RHRE	3
<i>Richardia scabra</i> L.	Rubiaceae	RISC	1
<i>Ruellia caroliniensis</i> (J.F. Gmel.) Steud.	Acanthaceae	RUCA	5
<i>Serenoa repens</i> (Bartram) Small	Arecaceae	SERE	9
<i>Setaria pumila</i> (Poir.) Roem. & Schult.	Poaceae	SEPU	1
<i>Smilax auriculata</i> Walter	Smilacaceae	SMAU	29
<i>Smilax</i> spp	Smilacaceae	SMSP	3
<i>Smilax tamnoides</i> L.	Smilacaceae	SMTA	1
<i>Solidago</i> spp	Asteraceae	SOSP	4
<i>Sorghastrum secundum</i> (Elliott) Nash	Poaceae	SOSE	29

APPENDICES (CONTINUED)

<i>Stillingia sylvatica</i> L.	Euphorbiaceae	STSY	1
<i>Tephrosia florida</i> (F.G. Dietr.) C.E. Wood	Fabaceae	TEFL	1
<i>Trichostema dichotomum</i> L.	Lamiaceae	TRDI	1
<i>Trifolium repens</i> L.	Fabaceae	TRRE	1
<i>Vaccinium darrowii</i> Camp.	Ericaceae	VADA	1
<i>Vaccinium myrsinites</i> Lam.	Ericaceae	VAMY	8
<i>Viola primulifolia</i> L.	Violaceae	VIPR	1
<i>Vitis aestivalis</i> Michx.	Vitaceae	VIAE	3
<i>Zanthoxylum clava-herculis</i> L.	Rutaceae	ZACL	1

¹ Ten distinct but unidentified species, found just once (or something like "found 1-2 times"), were also part of the data analyzed.