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James J. Angelo
University of Central Florida

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CHARACTERIZING THE VERTICAL STRUCTURE AND STRUCTURAL DIVERSITY OF
FLORIDA OAK SCRUB VEGETATION USING DISCRETE-RETURN LIDAR

by

JAMES J. ANGELO
B.A. Duke University, 1993

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ABSTRACT

Vertical structure, the top-to-bottom arrangement of aboveground vegetation, is an important component of forest and shrubland ecosystems. For many decades, ecologists have used foliage height profiles and other measures of vertical structure to identify discrete stages in post-disturbance succession and to quantify the heterogeneity of vegetation. Such studies have, however, required resource-intensive field surveys and have been limited to relatively small spatial extents (e.g., <15 ha). Light detection and ranging (lidar) is an active remote sensing technology with enormous potential to characterize the three-dimensional structure of vegetation over broad spatial scales.

In this study, discrete-return lidar data were used to create vertical profiles for over 500 vegetation patches on approximately 1000 ha of an oak scrub landscape in the Kennedy Space Center/Merritt Island National Wildlife Refuge area on the east-central coast of Florida. Non-parametric multivariate analysis of variance (NPMANOVA) tests detected significant differences among the profiles belonging to the four predominant land use/land cover (LULC) types in the study area. For the dominant LULC category (*Herbaceous upland non-forested*), pairwise NPMANOVA comparisons indicated that there were significant differences between vertical profiles for some of the distinct time since fire (TSF) values. Measures of vertical structural diversity (VSD) were calculated from the vertical profiles and then null, linear, and quadratic models relating VSD to TSF were compared via an Akaike information criterion (AIC) model selection procedure. As predicted by the Intermediate Disturbance Hypothesis, the quadratic model was the best model for the *Herbaceous upland non-forested* LULC category, but it explained less than 3% of the total variation in VSD. When fire frequency was considered in conjunction with TSF for this LULC category, however, the model that was quadratic in both

predictor variables was the best model among the candidates and explained over 6% of the total variation in VSD.

These results support the Extended Keystone Hypothesis, which predicts that disturbance generates discrete structural patterns across landscapes, and the Intermediate Disturbance Hypothesis, since the VSD of the predominant LULC category was maximized at intermediate levels of fire disturbance (i.e., intermediate values of TSF and/or fire frequency). In addition to demonstrating the ability of discrete-return lidar to characterize the vertical structure of vegetation at the landscape scale, this research has potential management implications. Using the techniques developed in this study, practitioners can compare the vertical structure of managed ecosystems to reference natural systems to evaluate the efficacy of managed disturbance regimes.

For my parents

ACKNOWLEDGMENTS

brother, Joey, for helping me persevere through some very difficult times. And, finally, for my little sister, Jennifer: you may be gone, but you are never forgotten!

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LIST OF ACRONYMS/ABBREVIATIONS

AIC	Akaike Information Criterion
ALTM	Airborne Laser Terrain Mapper
ANOVA	Analysis of Variance
DEI	Distance of Edge Influence
DEM	Digital Elevation Model
EKH	Extended Keystone Hypothesis
FHD	Foliage Height Diversity
IDH	Intermediate Disturbance Hypothesis
KSC/MINWR	Kennedy Space Center/Merritt Island National Wildlife Refuge
LIDAR	Light Detection and Ranging
LULC	Land Use and Land Cover
MANOVA	Multivariate Analysis of Variance
NASA	National Aeronautics and Space Administration
NCALM	National Center for Airborne Laser Mapping
NPMANOVA	Non-parametric Multivariate Analysis of Variance
SE	Standard Error
SJRWMD	St. Johns River Water Management District
TSF	Time Since Fire
VSD	Vertical Structural Diversity

CHAPTER 1: INTRODUCTION

In the most general sense of the concept, biological diversity (or "biodiversity") refers to the variety of life at all levels of ecological organization (Hunter 1999). Thus, genotypic diversity among individual organisms of the same species interacts with the environment to generate the phenotypic variability observed at the population level, and then variation among all of the populations of the different species living in a particular area creates diversity at the community level. Together, all of the biological communities with their associated abiotic components produce ecosystem diversity at the landscape level, and so on up the organizational hierarchy. But while genetic, species, and ecosystem diversity are fundamental components of any definition of biological diversity, biodiversity represents much more than the number of entities (whether they be genes, species, or ecosystems) present in a given area (Noss 1990).

Franklin et al. (1981) identified the following three primary attributes of forest ecosystems: composition, function, and structure; subsequently, Noss (1990) proposed that the biodiversity of any level of the ecological hierarchy could be divided into compositional, functional, and structural components. Compositional diversity refers to the identity and variety of entities at a given level (e.g., genetic diversity or species diversity), functional diversity encompasses ecological and evolutionary processes (e.g., gene flow or natural disturbances), and structural diversity involves "the physical organization or pattern of a system," (e.g., genetic structure or landscape patterns) (Noss 1990). In the context of forest ecosystems, structural diversity can be thought of as the horizontal and vertical distribution of plants. For example, vertical structural diversity might be measured as the variation in vegetation heights (Roberts and

Gilliam 1995). As discussed by Franklin (1988) and Noss (1990), ecologists and conservation biologists have focused primarily on maintaining compositional diversity, while often overlooking the loss of functional and structural diversity caused by the disruption of ecological processes and/or the structural homogenization and simplification of ecosystems. In an encouraging trend, researchers in recent years have devoted an increasing amount of attention to understanding the importance of functional diversity in maintaining vital ecosystem processes and services (Hooper et al. 2005).

While the importance of structural diversity is still not emphasized to the extent of compositional and functional diversity in the biodiversity conservation debate, some of the earliest pioneers in the field of ecology recognized the vital role of structure in natural systems. In his early-20th century monograph on ecological succession, Victor Shelford (1912) pointed to the existence of "distinct growth-form strata" in nearly all terrestrial plant assemblages. He went on to note that these different strata offered variations in light, temperature, moisture, and other abiotic factors, thus promoting the existence of distinct species of animals at different levels of vegetation (Shelford 1912). W. C. Allee (1926) furthered the idea that the vertical heterogeneity of vegetation produced distinct strata of abiotic and biotic resources within forests, thereby generating vertically stratified animal communities as well. Decades later, MacArthur and MacArthur (1961) provided empirical evidence for the hypothesized relationship between vertical structural diversity and species diversity. In their oft-cited study of mixed-wood temperate forests in the northeastern U.S., they found a positive correlation between bird species diversity and the "foliage height diversity" (FHD) of forest patches (MacArthur and MacArthur 1961).

The FHD method developed by MacArthur and MacArthur (1961) requires measuring the proportions of total leaf area at different height intervals and then using the Shannon index (Shannon 1948) to calculate diversity based on the relative abundance of the foliage occurring at different heights. Over the half-century since its introduction, FHD has become one of the most widely-used indices of one aspect of structural diversity in forest ecosystems, that of "vertical structure" (McElhinny et al. 2005). Brokaw and Lent (1999) defined vertical structure as "the bottom to top configuration of aboveground vegetation within a forest stand (a relatively homogeneous area of forest with a common history of development)." Research from a wide variety of forest ecosystems has indicated that vertical structure can change dramatically over the course of ecological succession (Aber 1979, Brokaw and Lent 1999). For example, studies using both field-collected and remotely-sensed data have shown that old-growth stands of Douglas-fir forests in the Pacific Northwest contain a greater number of canopy layers and a higher diversity of tree heights than younger stands (Franklin et al. 1981, Lefsky et al. 1999).

Some of the cornerstones of modern ecological theory hypothesize that disturbance is a key mechanism in producing structure and maintaining diversity at the ecosystem level (Roberts and Gilliam 1995). Connell (1978) proposed the Intermediate Disturbance Hypothesis (IDH), in which the levels of diversity in a given ecosystem are maximized at intermediate levels of disturbance. While ecologists have tested the IDH for a wide variety of ecosystems and disturbance types [e.g., see reviews in Mackey and Currie (2001), Shea et al. (2004), and Hughes et al. (2007)], the diversity measured in these studies has primarily been compositional diversity (species richness, species evenness, or some combination of both). In principle, however, the IDH may also be applicable to the structural diversity of vegetation. While Connell (1978)

proposed that disturbance increased diversity by reducing the dominance of competitively superior species in an ecosystem, another possible mechanism is that disturbance increases habitat heterogeneity and thus promotes resource partitioning (Denslow 1980, 1985). Based on the IDH, therefore, one might predict that the greatest diversity in vertical structure—as defined, for example, by the number of vegetation strata—would be present at intermediate levels of disturbance (Brokaw and Lent 1999). At least some empirical evidence for such a relationship has been reported in the literature. In their study of northern boreal forests, for example, Brassard et al. (2008) noted that the highest diversity of tree heights in broadleaf stands occurred at intermediate ages of time since stand-replacing fire.

While the IDH addressed how the process of disturbance might affect diversity, Holling's (1992) Extended Keystone Hypothesis (EKH) proposed that all terrestrial ecosystems are organized by a small set of ecological processes (so-called "structuring processes"), each of which operates at a characteristic spatiotemporal scale. At the smallest scales, biotic processes such as plant growth and competition are the dominant structuring processes; at the largest scales, on the other hand, abiotic processes such as climate and geomorphology tend to dominate. A corollary to the EKH is that certain disturbances are the key structuring processes at the meso-scale (i.e. spatial scales of tens of meters to kilometers). These processes, known as "contagious disturbance processes," are characterized by their spatially spreading character and their ability to transfer patch-scale dynamics into discrete structural patterns at larger scales (Holling 1992). One such contagious disturbance process, fire, has long been recognized for its ability to generate discrete structural patterns in vegetation at various scales (Romme 1982, Peterson 2008). Empirical tests of the EKH have revealed that structural patterns generated by

fire and other contagious disturbance processes can be detected from topographic and vegetation data (Szabo and Meszena 2006). Van Pelt and Franklin (2000) developed methods to detect discontinuities in vertical vegetation profiles derived from field data; however, such methods are time-consuming and resource-intensive and thus may have limited applicability at spatial scales larger than individual forest stands (Gagné et al. 2008). While imagery attained via passive remote sensing facilitates analysis at broader scales (Turner et al. 1994), it can only delineate two-dimensional surface patterns and the optical "signals" of disturbance (e.g., fire scars) become increasingly obscured as vegetation recovers from the disturbance (DeFries 2008). As a result, the effectiveness of passive imagery may be limited in ecosystems characterized by rapid post-disturbance regeneration of vegetation (Shao and Duncan 2007, Duncan et al. 2009).

Airborne light detection and ranging (lidar) is an active remote sensing technology that is capable of capturing the three-dimensional structure of vegetation at high resolutions (both vertical and horizontal) and over relatively broad spatial scales (Lefsky et al. 2002, Vierling et al. 2008). While numerous researchers have reported on the ability of lidar data to characterize the vertical structure of vegetation [see Omasa et al. (2007) for a recent review], most ecologically-oriented studies incorporating lidar have relied on relatively simple lidar-derived metrics, such as canopy height (Zimble et al. 2003, Hurtt et al. 2004). As Hurtt et al. (2004) noted, however, there is potentially an enormous wealth of information about the state of terrestrial ecosystems contained in the vertical profiles of vegetation derived from lidar data. Næsset (2004) introduced a technique for generating vertical profiles from discrete-return lidar data by counting the density of laser returns occurring in bins of equal height in the column that extends vertically over an area with a fixed horizontal cell size. More recently, researchers have employed vertical profiles

derived from discrete-return lidar data in a growing number of applied ecological studies, such as the classification of land cover in the wildland-urban interface (Koetz et al. 2008), the characterization of successional states in a multistory forest (Falkowski et al. 2009), and the prediction of the time since last disturbance in a shrubland ecosystem (Angelo et al. 2010).

Florida oak scrub is potentially an excellent model system in which to test the ability of lidar remote sensing to characterize the vertical structure of vegetation at landscape scales and the efficacy of using lidar-derived profiles of vertical structure to test the predictions of the EKH and the IDH. Oak scrub, which is also known as "scrubby flatwoods" or "oak-saw palmetto scrub," is a fire-dependent shrubland community that requires relatively frequent burning (every 5-20 years) to maintain its characteristic structure of numerous sandy openings, a sparse herb layer, little or no tree cover, and a relatively dense shrub layer at heights of 1 to 2 m (Duncan et al. 1999, Menges 1999). Unlike some other types of Florida scrub, however, oak scrub communities are dominated by species that resprout rapidly after fire and are not prone to invasion by hardwood hammock species in the prolonged absence of fire (Schmalzer and Hinkle 1987, 1992). Consequently, the post-fire response of these communities is characterized almost exclusively by structural changes, such as increased growth in vegetation height and biomass, with little-to-no change in species composition. Due to these characteristics, oak scrub may represent an ideal system in which to observe the effects of disturbance on vertical structure without the confounding influence of the compositional changes associated with traditional post-fire succession (Schmalzer and Hinkle 1992).

In this study, I used discrete-return lidar to create vertical profiles of the vegetation patches in an oak scrub landscape on the east-central coast of Florida, and then I used these

profiles to test predictions of the EKH and the IDH. In accordance with the EKH, I predicted that vegetation patches with the same land use/land cover (LULC) category but possessing different time since fire (TSF) values would have vertical profiles that are significantly different from each other. Next, I computed indices of vertical structural diversity (VSD) from the vertical profiles to test the IDH. Finally, in accordance with the IDH, I predicted that vegetation patches from the same LULC category would exhibit the highest levels of VSD at intermediate levels of disturbance, as represented by the time since fire.

CHAPTER 2: METHODS

2.1 Study Area

The study area was located in east-central Florida on the Atlantic coast of the United States and contained two sites separated by a distance of just over 1.5 km (Figure 1). Together, these two sites occupied a combined area of almost 10 km^2 of federally-owned land near the southern boundary of the Kennedy Space Center/Merritt Island National Wildlife Refuge (KSC/MINWR). The elevation in the area ranged from 1 to 3.5 m above sea level due to the ridge-swale topography formed from relict beach dunes of the Pleistocene (Schmalzer and Hinkle 1987). Upland areas (also known as scrub ridges) were characterized by well-drained soils and evergreen shrub oaks, primarily sand live oak (*Quercus geminata* Small), Chapman's oak (*Q. chapmanii* Sarg.), and myrtle oak (*Q. myrtifolia* Willd.). Mesic flatwoods were dominated by shrubs in the understory, including saw palmetto (*Serenoa repens* (Bartram) Small) and lyonia (*Lyonia* spp.), with interspersed swale marshes (*Spartina bakeri* Merr.) and sparse clusters of open-canopy slash pine (*Pinus elliottii* Engelm.) (Duncan et al. 1999). This combination of scrub communities and pine flatwoods is sometimes called "oak-saw palmetto scrub" or "scrubby flatwoods," but shall be referred to exclusively as "oak scrub" for the remainder of this manuscript (*sensu* Schmalzer and Hinkle 1987).
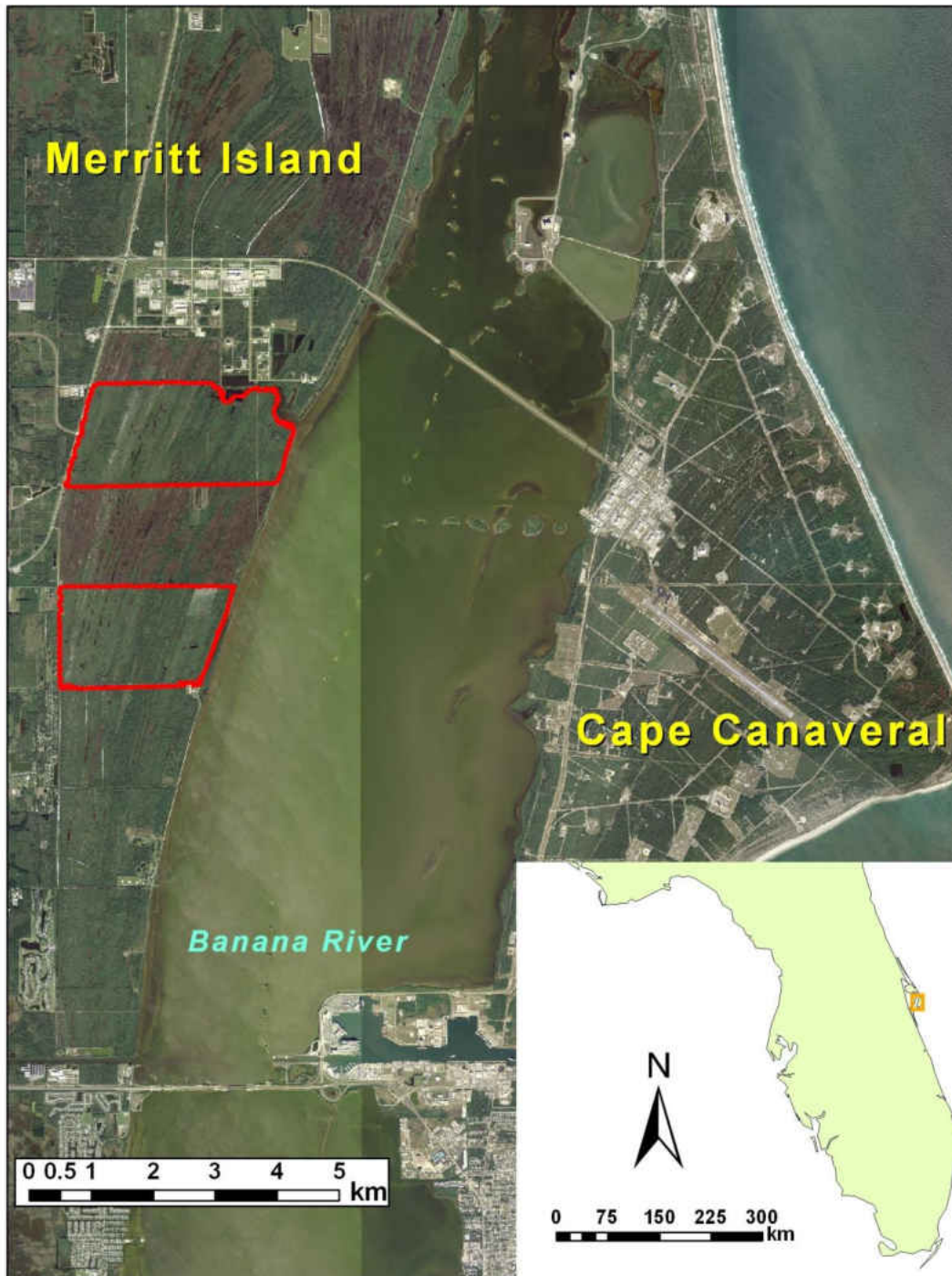
Figure 1: The study area location on the east-central coast of Florida (inset), with north and south sites outlined in red (main map).

Because the study area encompassed a landscape of heterogeneous ecosystems, the 2004 St. Johns River Water Management District (SJRWMD) Land Use and Land Cover (LULC) dataset was used to control for *a priori* differences in vertical structure among the major vegetation types (SJRWMD 2006). The most dominant LULC category was *Herbaceous upland non-forested*, which comprised almost 63% of the study area, followed by *Wetland hardwood forests* (≈17%), *Vegetated non-forested wetlands* (≈13%), *Shrub and brushland* (≈4%), and *Surface water collection ponds* (≈2%) (Figure 2). The remaining area consisted of a variety of other LULC categories that together comprised just over 1% of the study area. While the 2004 SJRWMD dataset was the most recent publically-available LULC data for the study area, some of the category names in this dataset may not accurately reflect the actual vegetation on the ground. For example, the *Herbaceous upland non-forested* category appears to encompass areas that are better described as "oak scrub of short stature," and the *Shrub and brushland* category seems to encompass areas more appropriately described as "oak scrub of taller stature" (R. Hinkle and R. Noss, pers. comm.). For the sake of consistency, however, the original category names from the 2004 SJRWMD LULC dataset are used exclusively throughout this manuscript.

Wildfire was suppressed throughout much of the KSC/MINWR area from the 1950s until 1981, when the U.S. Fish and Wildlife Service instituted a prescribed burning program to reduce the buildup of vegetative fuel loads (Duncan et al. 2009). As described in Duncan et al. (2009), the managed fire regime at KSC/MINWR has been documented extensively with a combination of written records of each burn, as well as fire boundaries delineated from historic satellite imagery. The time since fire (TSF) values in the study area ranged from 1 to >27, with the latter category including all areas that had not been burned since 1981 (Figure 3). Fire frequencies

ranged from 0, for those patches that had not been burned, to a maximum of 6 times since 1981 (Figure 4).

Figure 2: Map of the land use/land cover (LULC) categories in the study area (HUN = *Herbaceous upland non-forested*, SB = *Shrub and brushland*, WHF = *Wetland hardwood forests*, VNW = *Vegetated non-forested wetlands*, and Water = *Surface water collection ponds*).

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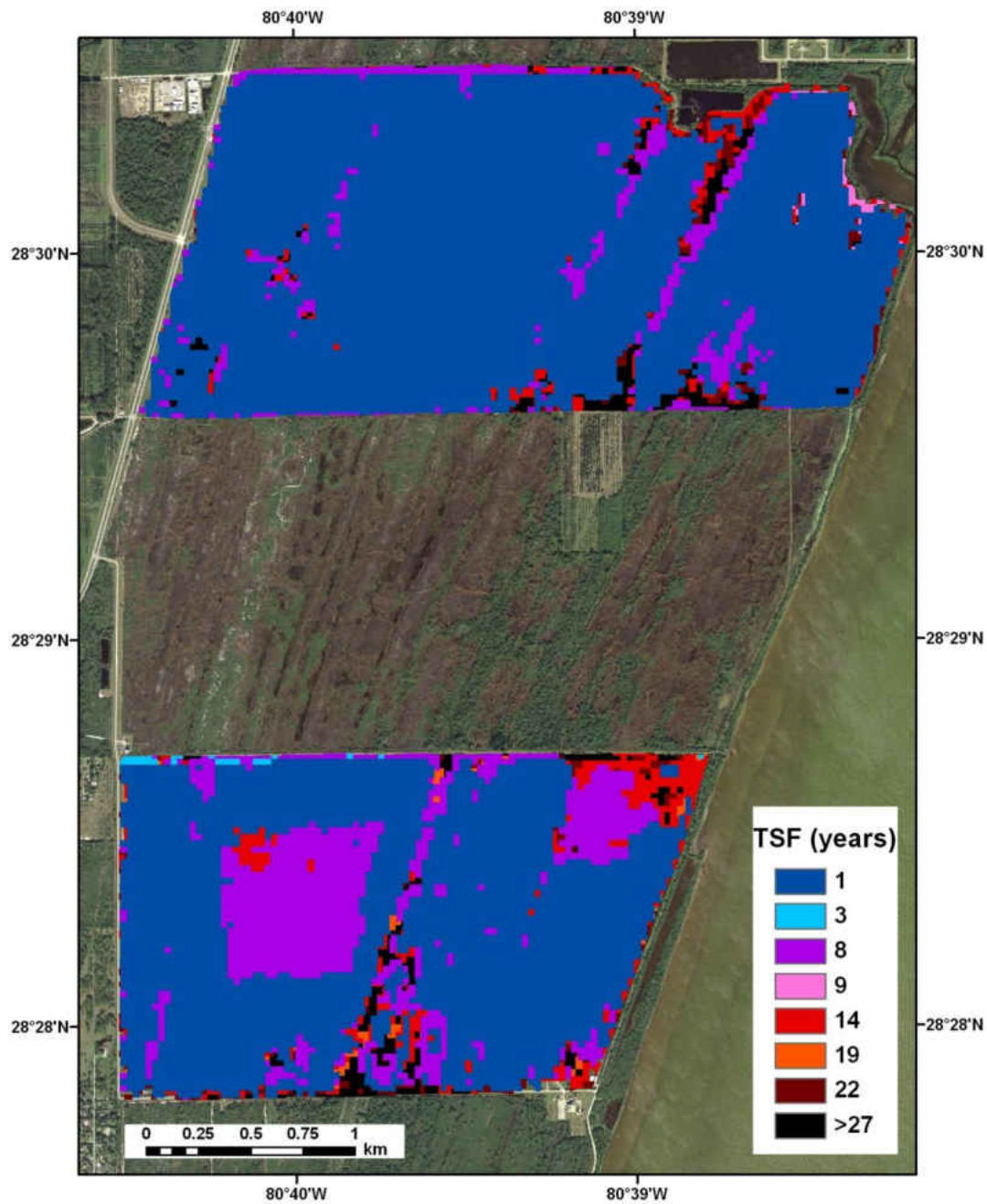
Figure 3: Time since fire (TSF) of prescribed burns in the study area. The color of each pixel indicates the TSF, in years relative to 2008, of the last known prescribed burn. The class designated as ">27" indicates those areas that have not been burned since 1981 (Duncan et al. 2009).

13
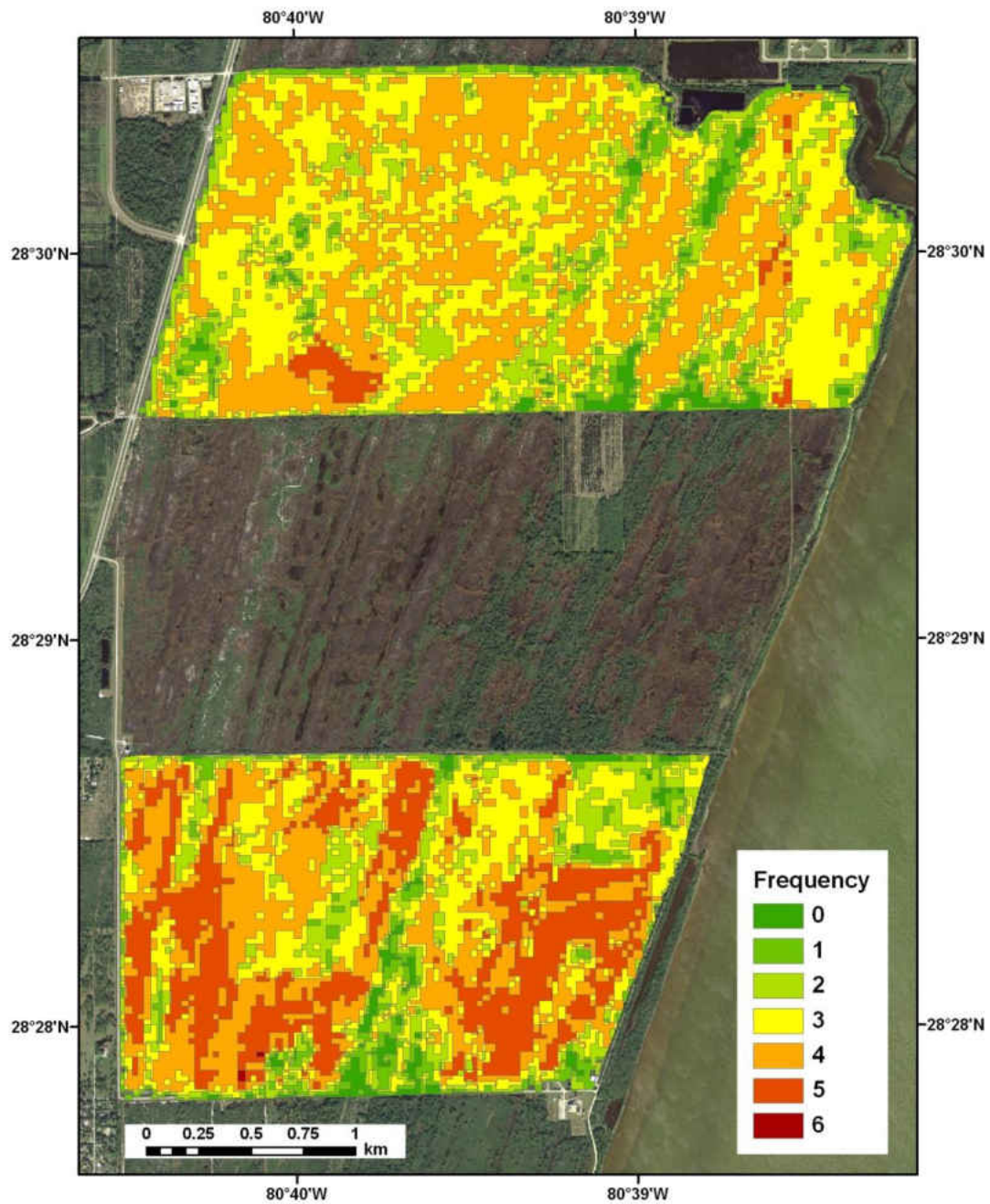
Figure 4: Frequency of prescribed burns in the study area. The color of each pixel indicates the number of times that the area has been burned since 1981 (Duncan et al. 2009).

2.2 Lidar Data Acquisition and Processing

The lidar data used for this study were acquired by the National Center for Airborne Laser Mapping (NCALM) in June of 2008 with an Optech GEMINI Airborne Laser Terrain Mapper (ALTM) mounted on a Cessna Skymaster airplane. The ALTM operated at a wavelength of 1047 nm with a pulse repetition rate of 70 kHz, yielding a laser return density of approximately 4.2 points per m^2 and an average positional error of <0.4 m in both the horizontal and vertical directions (M. Sartori, pers. comm.). NCALM delivered the lidar point cloud data in industry-standard .LAS format, with individual returns classified as "ground," "non-ground," or "low noise." From the point cloud data, a high-resolution (1 m) bare earth digital elevation model (DEM) was produced using FUSION lidar-processing software (McGaughey 2009) to apply median smoothing filters and spike removal algorithms to the ground points.

Next, the bare earth DEM and the non-ground lidar points were input to FUSION to generate point clouds of vegetation returns with their heights normalized to the distance above the ground. Because the study area contained very few human-made structures, it was assumed that all laser returns classified as "non-ground" were reflected from vegetation. The returns from these vegetation point clouds were then binned vertically to create representative profiles of the vertical structure (hereafter referred to as "vertical profiles") for all of the vegetation patches in the study area. Vegetation patches were defined as in Petraitis et al. (1989): "We take a *patch* to be *a contiguous area in which the effect of a disturbance is uniform and the subsequent dynamics are similar* [italics in original]." This is analogous to the concept of a "forest stand" as defined by Brokaw and Lent (1999): "a relatively homogeneous area of forest with a common history of

development." Each unique combination of LULC and TSF was, therefore, considered to be an independent vegetation patch. For each patch, bins were created containing the number of returns recorded in every 1 m height interval from 0 to 15 m above the ground, with the last bin containing all returns above 15 m. Finally, the number of returns in each bin was divided by the area of the patch (in m^2) to produce the patch's vertical profile (Figure 5).

a)

Patch Area = 769.16 m²

b)

Height Above Ground (m)	Number of Returns	Return Density (per m²)
> 15	0	0
14 – 15	0	0
13 – 14	0	0
12 – 13	0	0
11 – 12	0	0
10 – 11	18	0.02
9 – 10	92	0.12
8 – 9	149	0.19
7 – 8	276	0.36
6 – 7	280	0.36
5 – 6	202	0.26
4 – 5	127	0.17
3 – 4	165	0.21
2 – 3	112	0.15
1 – 2	634	0.82
0 – 1	61	0.08
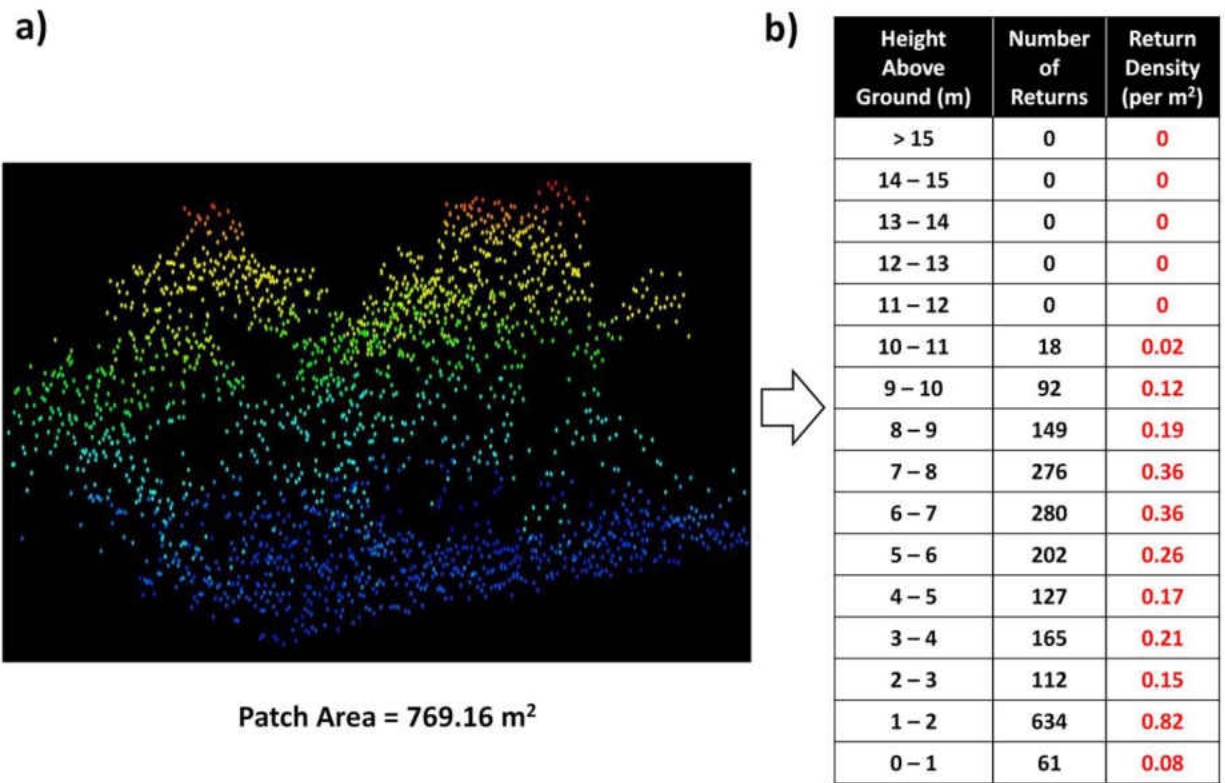
Figure 5: Creation of a vertical profile for a vegetation patch in the study area. a) Original point cloud of vegetation (i.e., non-ground) lidar returns, with red points indicating highest returns and blue points indicating returns closest to the ground. b) Table showing raw counts (second column) and densities (third column) of vegetation returns in each 1 m vertical height bin.

2.3 Distance of Edge Influence Estimation

The sites analyzed in this study are bordered on all of their edges by paved roads. Such "maintained" edges frequently produce dense sidewalls of vegetation in the edge zone between the road and the forest interior (Harper et al. 2005), with vegetation structural responses extending up to 50 m from the edge (Ries et al. 2004). In order to estimate the distance of edge influence (DEI) attributable to the roads surrounding the study sites, a modified version of the "critical values" approach developed by Harper and Macdonald (2001, 2002) was taken. In essence, this method estimates the DEI by comparing the vegetation structure in buffer zones created at a series of distances from the edge to that of an area designated as the interior, with the DEI then considered to be the set of distances where the structure in the edge area is significantly different from that of the interior (Harper and MacDonald 2001).

To estimate the DEI in the study area, the interior vegetation was defined as those areas 100 m or greater from the roads. This distance was chosen because nearly all studies of temperate forest ecosystems have determined the DEI of forest structure to be less than 100 m from the edge (Harper and Macdonald 2002, Harper et al. 2005). ArcGIS, Version 9.3 (ESRI Inc., Redlands, California, USA) was then used to create the interior vegetation patches by buffering a distance of 100 m inward from the boundaries of all areas with a LULC classification of *Herbaceous upland non-forested* and having a TSF of 1 year (as shown in Figures 2 and 3, these vegetation patches comprised the largest extent of both study sites). Next, edge vegetation

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patches were created by buffering at distances of 20 m, 40 m, 50 m, 60 m, and 80 m from the site boundaries. Finally, vertical profiles were generated for both the edge and interior vegetation patches according to the process described in the preceding section.

To test for significant differences between the edge profiles and the interior profiles at each of the edge distances, a non-parametric multivariate analysis of variance (NPMANOVA) was performed using the *vegan* package of R (Oksanen et al. 2009). NPMANOVA is a powerful technique that partitions the variance in a set of potentially non-independent simultaneous response variables in a manner analogous to a parametric multivariate analysis of variance (MANOVA) (Anderson 2001). This approach is particularly well-suited for multivariate ecological datasets, such as discrete abundance and density data, whose distributions often fail to meet the assumptions of multivariate normality required by parametric MANOVA tests (McCune and Grace 2002). First, a dissimilarity index is used to calculate the pairwise distances among all the observations and to produce a "pseudo F-ratio" (i.e., the mean squared difference among groups divided by the mean squared difference within groups). Then, the observations are randomly permuted to generate a distribution of the test statistic under the null hypothesis of no differences among groups, and this distribution is used to assess the statistical significance of the observed differences (Anderson 2001). For all of the NPMANOVA tests performed in this study, the Jaccard dissimilarity index was used to calculate pairwise distances between observations, and 10,000 permutations were performed to test for statistical significance. The Jaccard index is a metric version of the Bray-Curtis dissimilarity index, which has been widely adopted in multivariate analyses of ecological community data (Anderson 2001, Oksanen et al. 2009).

2.4 Vegetation Profile Comparisons

After the DEI was estimated for the study area, each site was buffered by a distance equal to the estimated DEI from the road edge, and then only the interior regions of the study sites were utilized in the remaining analyses. To test for *a priori* differences in vertical structure among vegetation with different LULC classifications, ArcGIS was used to extract all areas belonging to the four predominant vegetation cover types in the study area (*Herbaceous upland non-forested*, *Wetland hardwood forests*, *Vegetated non-forested wetlands*, and *Shrub and brushland*). Then, vertical profiles for all vegetation patches were created and pairwise comparisons among the vertical profiles of the predominant LULC categories were performed with the NPMANOVA tests described above. A sequential Bonferroni procedure was used to maintain the family-wise Type I error rate at $\alpha = 0.05$ for the $c = 6$ pairwise comparisons among the four predominant LULC categories (Quinn and Keough 2002).

To test for the existence of discrete patterns in vertical structure among vegetation patches with different disturbance histories (as predicted by the EKH), the vertical profiles of the most dominant LULC category (*Herbaceous upland non-forested*) were grouped according to their TSF values, excluding profiles with TSF = 9 or TSF = 19. There were only $n = 4$ vegetation patches for both of these TSF values, compared to $n \geq 9$ for all other TSF values. Furthermore, the TSF = 9 patches were all clustered in the northeast corner of the study area and the TSF = 19 patches were all located in the southern site (Figure 3). Thus, it was unlikely that the TSF = 9 and TSF = 19 vegetation patches constituted a representative sample of these TSF values, and their profiles were excluded from the pairwise comparisons for the *Herbaceous upland non-*

forested LULC category. For the remaining TSF values in this LULC category (TSF = 1, 8, 14, 22, and >27), NPMANOVA tests were executed to detect significant differences among the vertical profiles based on TSF, again using a sequential Bonferroni procedure to maintain the family-wise Type I error rate at $\alpha = 0.05$ for the $c = 10$ pairwise comparisons.

2.5 Analyses of Vertical Structural Diversity

Testing the predictions of the IDH as it relates to the diversity of vertical structure in the study area was a two-step process. First, a measure of the vertical structural diversity (VSD) of each vegetation patch was calculated from the patch's vertical profile by taking the exponential of the Shannon index to convert the Shannon entropy function into a "true diversity" index (Jost 2006). This index, hereafter referred to as the Jost index, is given by the following equation:

$$VSD = \exp\left(-\sum_{i=1}^{s} p_i \ln p_i \right)$$

In the equation above, p_i is the proportion of vegetation returns in vertical height bin i, and s is the total number of height bins. This is analogous to the method used by MacArthur and MacArthur (1961) to calculate their FHD measure. Because the lidar returns from the vegetation may include woody parts as well as foliage (Weishampel et al. 2007), however, the term FHD would be inappropriate and the more general term VSD will be used instead.

Once the VSD indices were calculated for all of the vegetation patches, the patches were grouped by LULC and then a series of linear models were fit for each of the four predominant LULC categories to relate VSD to TSF. The first model was a null model consisting of two

parameters: an overall mean and an error term. The second model was a linear model with three parameters: a slope, an intercept, and an error term. The third model was a quadratic model that added a squared TSF parameter to the linear model. This quadratic model allowed for the possibility of a unimodal curve (i.e., a curve where diversity initially rises with TSF, reaches some maximum value, and then falls), which is the relationship predicted by the IDH. Akaike information criterion (AIC) scores were calculated for the models, and the model with the lowest AIC score in each LULC category was selected as the best fitting model (i.e., the "best model") for that category (Quinn and Keough 2002, Johnson and Omland 2004).

In addition to the time since the last disturbance, the frequency of disturbance is another potentially important component of an ecosystem's disturbance regime (Connell 1978, Denslow 1985, White and Pickett 1985). To test for a possible interaction between TSF and fire frequency, another series of models were fit for the *Herbaceous upland non-forested* LULC category. These models related VSD to some combination of TSF, fire frequency, and/or squared versions of these terms. In addition to additive models, models with interactions between the linear and/or quadratic terms were also considered. For these analyses, each patch classified as *Herbaceous upland non-forested* and possessing a unique combination of TSF and fire frequency was considered to have a unique disturbance history and, thus, to represent an independent vegetation patch. As with the models that considered only TSF, AIC scores were calculated for each of these models and the model with the lowest AIC score was selected as the best model.

CHAPTER 3: RESULTS

3.1 Distance of Edge Influence Estimation

The NPMANOVA comparisons of the vertical profiles indicated that the edge vegetation was significantly different from the interior vegetation at edge distances of 20 m ($F_{(1,57)} = 4.26$, $p < 0.001$) and 40 m ($F_{(1,58)} = 3.80$, $p = 0.004$) from the road (Figure 6). The edge profiles were not significantly different from the interior profiles at distances of 50 m or greater from the edge (50 m: $F_{(1,60)} = 1.12$, $p = 0.309$, 60 m: $F_{(1,61)} = 1.25$, $p = 0.244$, and 80 m: $F_{(1,62)} = 1.19$, $p = 0.276$). The height of the mean return in the interior vegetation was 3.35 m. At edge distances of 20 m and 40 m, the height of the mean return was higher (4.20 m and 3.51 m, respectively) than that of the interior. At an edge distance of 50 m, however, the height of the mean return (3.37 m) was almost the same as for the interior vegetation. Consequently, buffers of 50 m inward from the boundaries of the study sites were created and all subsequent analyses used only the vertical profiles created from the vegetation patches lying in the interior portions of the sites.
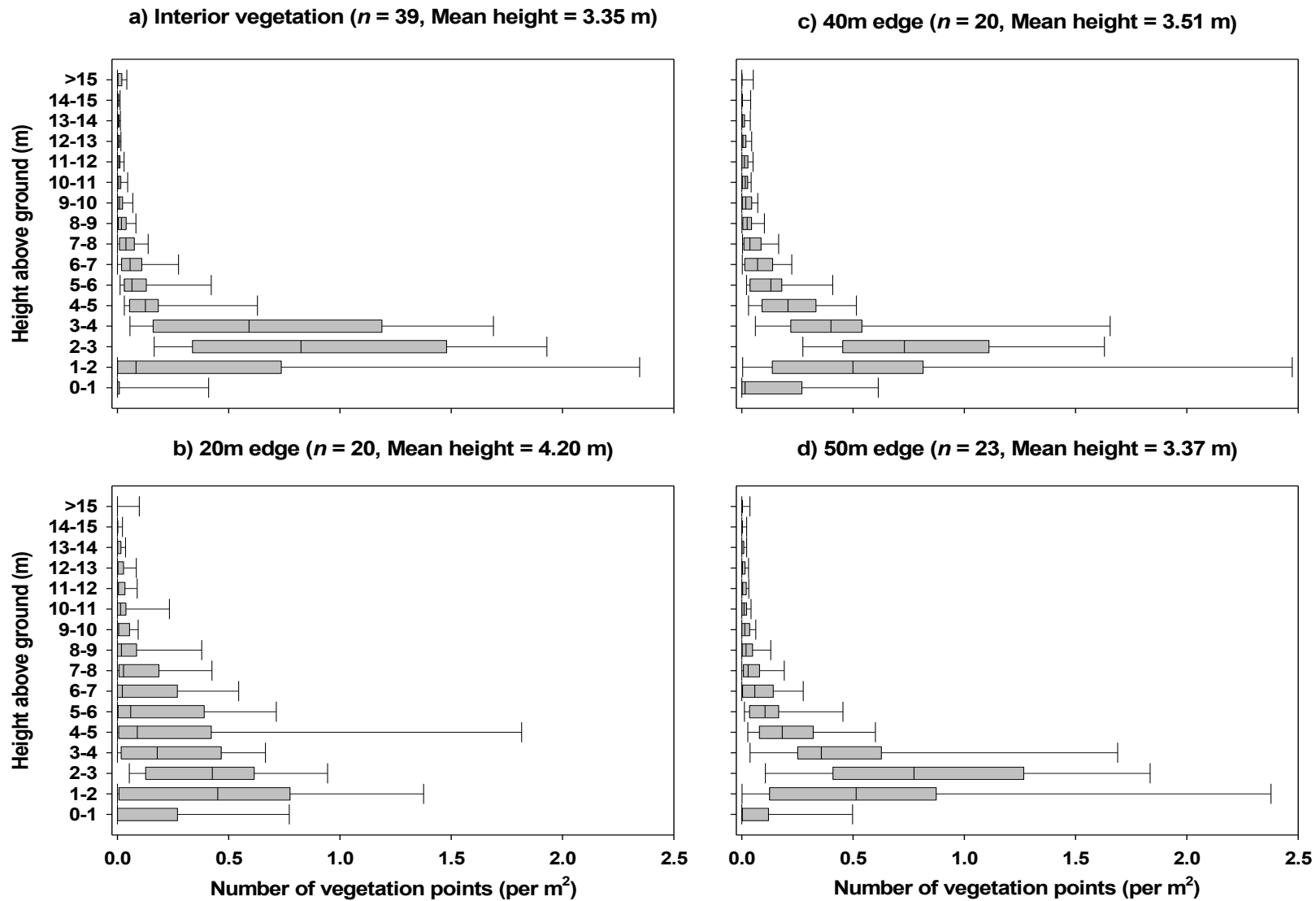
Figure 6: Vertical profiles used in distance of edge influence (DEI) analyses: a) interior profiles created by buffering 100 m inward from site boundaries, and edge profiles at distances of b) 20 m, c) 40 m, and d) 50 m. Bars represent 5th/95th percentiles, and *n* denotes the number of vegetation patches in each location.

The NPMANOVA comparisons of the four predominant LULC categories in the study area revealed that there were significant differences among the vertical profiles: $F_{(3,547)} = 17.72$, $p < 0.001$ (Figure 7). Furthermore, pairwise comparisons using the sequential Bonferroni adjustment indicated that all of the pairwise differences were significant at the family-wise Type I error rate of $\alpha = 0.05$ (Table 1).

Table 1: Pairwise comparisons of the vertical profiles from the four predominant land use/land cover (LULC) categories in the study area. Test statistics were "pseudo F-ratios" produced by the non-parametric multivariate analysis of variance (NPMANOVA) method of Anderson (2001) with Jaccard distance measures; p-values were generated using 10,000 random permutations of the observed data. All comparisons were significant at the family-wise Type I error rate of $\alpha = 0.05$ based on a sequential Bonferroni adjustment procedure.

LULC Category	Herbaceous upland non-forested	Shrub and brushland	Wetland hardwood forests	Vegetated non-forested wetlands
Herbaceous upland non-forested				
Shrub and brushland	$F_{(1,231)} = 6.94$ ($p < 0.001$)			
Wetland hardwood forests	$F_{(1,429)} = 42.43$ ($p < 0.001$)	$F_{(1,314)} = 13.49$ ($p < 0.001$)		
Vegetated non-forested wetlands	$F_{(1,233)} = 4.53$ ($p < 0.001$)	$F_{(1,118)} = 5.27$ ($p < 0.001$)	$F_{(1,316)} = 13.07$ ($p < 0.001$)	
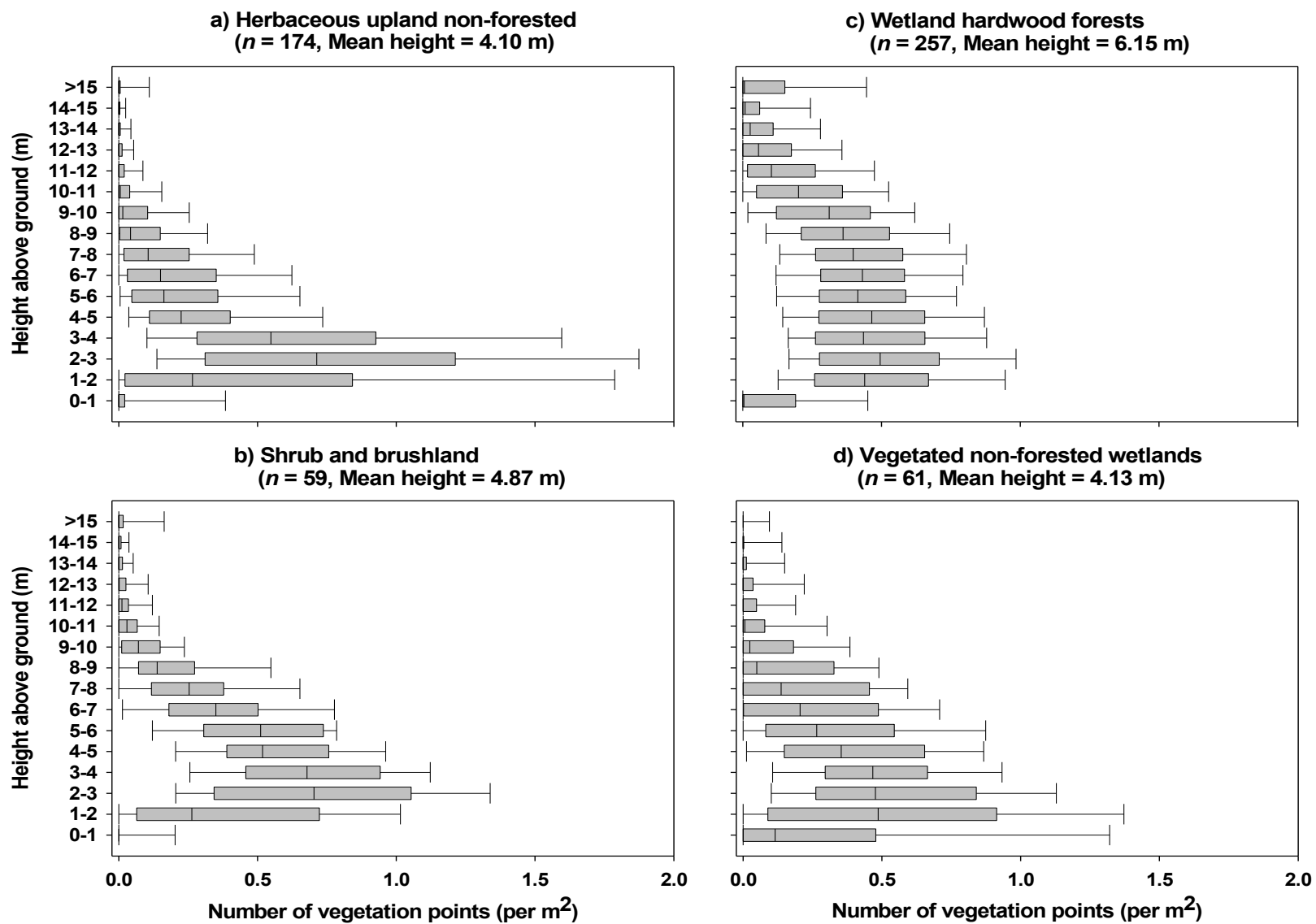
Figure 7: Vertical profiles for the predominant land use/land cover (LULC) categories in the study area. Bars represent 5th/95th percentiles, and *n* denotes the number of vegetation patches in each category.

For the most dominant LULC category in the study area (*Herbaceous upland non-forested*), the NPMANOVA results revealed that there were significant differences among the vertical profiles when grouped by TSF: $F_{(4,161)} = 2.15$, $p < 0.001$ (Figure 8). Pairwise comparisons using a sequential Bonferroni adjustment indicated that some, but not all, of the pairwise differences between TSF values were significant at the family-wise Type I error rate of $\alpha = 0.05$ (Table 2). The vertical profiles of the TSF = 1 class were significantly different from the vertical profiles of all the other TSF classes, except for those of TSF > 27. The only other significant pairwise difference in vertical profiles was between those of TSF = 8 and TSF = 22.

Table 2: Pairwise comparisons of the vertical profiles from the *Herbaceous upland non-forested* category grouped by time since fire (TSF), in years. Comparisons in bold were significant at the family-wise Type I error rate of $\alpha = 0.05$ using a sequential Bonferroni adjustment procedure. All other comparisons were not significant after the sequential Bonferroni adjustment.

TSF	*1*	*8*	*14*	*22*	*>27*
1					
8	$F_{(1,114)} = 3.36$ (**p = 0.002**)*				
14	$F_{(1,54)} = 3.08$ (**p = 0.005**)*	$F_{(1,106)} = 1.60$ ($p = 0.094$)			
22	$F_{(1,47)} = 2.94$ (**p = 0.005**)*	$F_{(1,99)} = 2.77$ (**p = 0.003**)*	$F_{(1,39)} = 1.99$ ($p = 0.014$)		
>27	$F_{(1,39)} = 0.97$ ($p = 0.427$)	$F_{(1,91)} = 1.03$ ($p = 0.381$)	$F_{(1,31)} = 1.18$ ($p = 0.256$)	$F_{(1,24)} = 0.96$ ($p = 0.468$)	
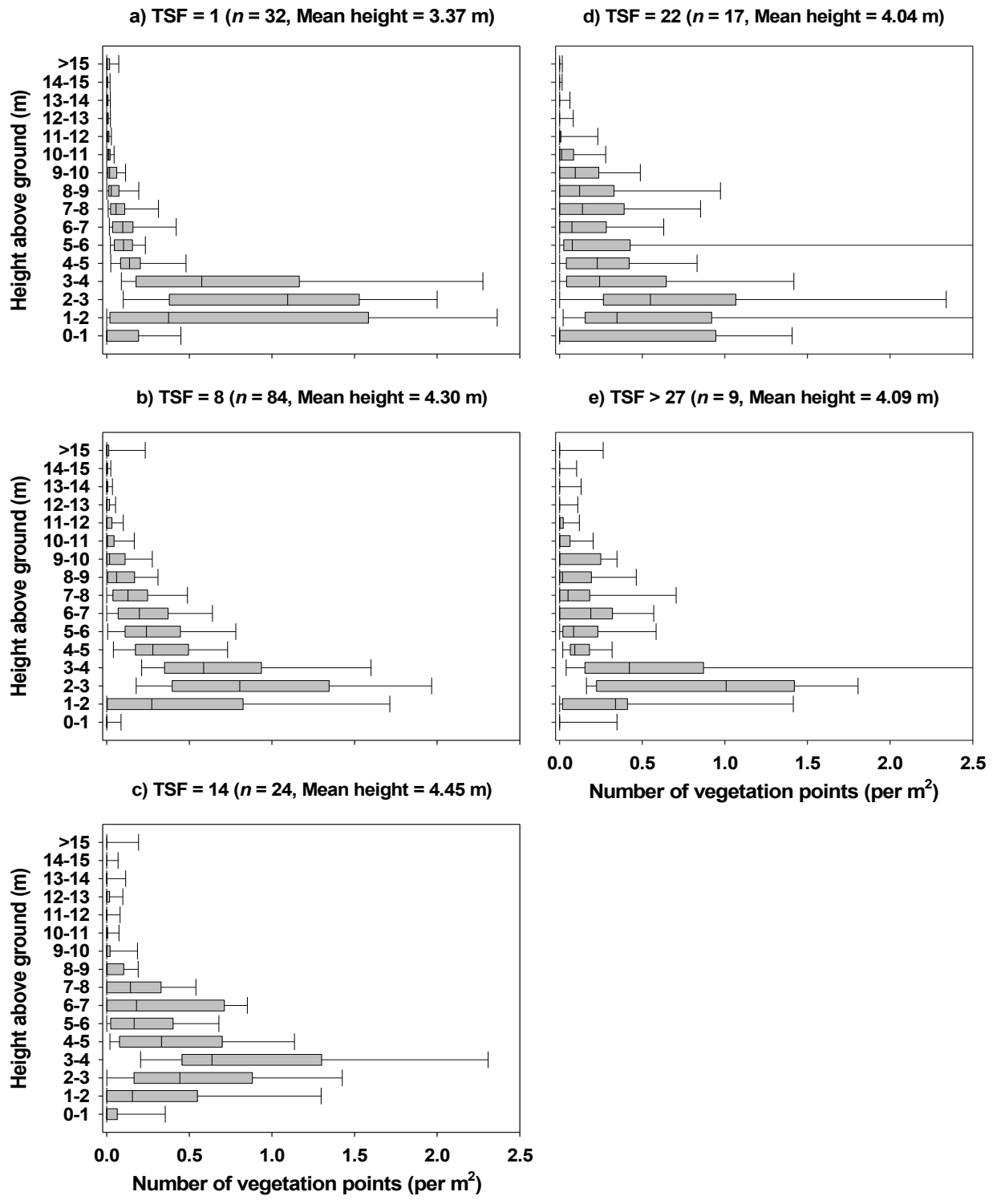
Figure 8: Vertical profiles from the *Herbaceous upland non-forested* category, grouped by time since fire (TSF), in years. Bars represent $5^{th}/95^{th}$ percentiles, and *n* is number of patches.

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3.3 Analyses of Vertical Structural Diversity

The Jost indices of VSD calculated for the four predominant LULC categories in the study area were distributed approximately normally within each category; consequently, a parametric one-way ANOVA with a Tukey's HSD test (Quinn and Keough 2002) was used to perform pairwise comparisons among the different LULC categories at a nominal family-wise Type I error rate of $\alpha = 0.05$ (Figure 9). The *Wetland hardwood forests* category had the highest average VSD, with a mean Jost index (10.46) that was significantly higher than that of the other three LULC categories ($p < 0.001$). The *Shrub and brushland* category had the second highest mean VSD (7.48), and was significantly higher than the *Herbaceous upland non-forested* (mean VSD = 5.69, $p < 0.001$). The mean VSD of the *Vegetated non-forested wetlands* LULC category (6.94) was less than, but not significantly different from ($p > 0.05$), that of the *Shrub and brushland* category. There was a significant positive correlation between VSD and the mean height of return (Pearson's $r = 0.827$, $p < 0.001$), but over 30% of the variation in VSD was unexplained by the mean height.
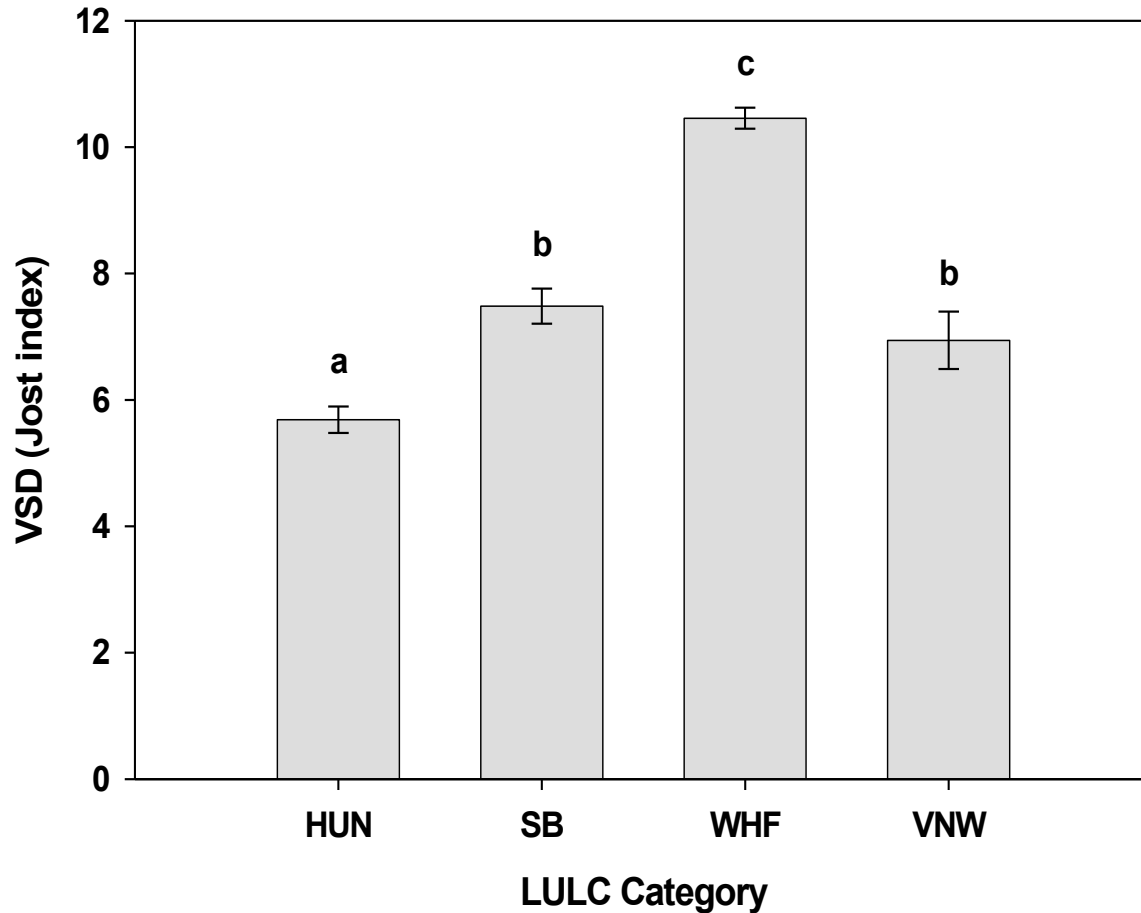
Figure 9: Comparison of vertical structural diversity (VSD) indices for the four predominant land use/land cover (LULC) categories in the study area (HUN = *Herbaceous upland non-forested*, SB = *Shrub and brushland*, WHF = *Wetland hardwood forests*, and VNW = *Vegetated non-forested wetlands*). Wide bars indicate mean values and error bars indicate ± 1 SE. Letters above each bar denote groups with significantly different mean levels of diversity, based on the results of a Tukey's HSD test with a nominal family-wise Type I error rate of α = 0.05.

For the *Herbaceous upland non-forested* LULC category, the quadratic model (VSD = 4.336 + 0.244* *TSF* – 0.008* *TSF²*) was the best model with an AIC score of 806.47, compared to AIC scores of 809.16 and 809.41 for the null and linear models (Table 3, Figure 10a). The overall quadratic model was significant ($F_{(2,163)}$ = 3.35, p = 0.038) with an adjusted R^2 of 0.028, and all of the model's coefficients were also significant. Given the AIC scores for the quadratic, null, and linear models, the corresponding Akaike weights (W_i) were 0.670, 0.175, and 0.154, respectively. This indicates that the probability that the quadratic model was the best model ($\approx$ 67%) among the candidate models for this LULC category was almost four times greater than that of the next-best model, the null model ($\approx$ 17.5%).

For the *Shrub and brushland* LULC category, the linear model (VSD = 8.373 - 0.072* *TSF*) was the best model (Table 3, Figure 10b). This model was significant ($F_{(1,57)}$ = 4.72, p = 0.034) and had an adjusted R^2 of 0.060. Based on the AIC scores for the linear, quadratic, and null models (257.47, 259.22, and 260.16, respectively), the corresponding W_i were 0.596, 0.249, and 0.155, indicating that the probability that the linear model was the best model ($\approx$ 60%) among the candidate models was over twice that of the quadratic model ($\approx$ 25%).

Neither the quadratic nor the linear models were statistically significant for the remaining two LULC categories (Table 3). For the *Wetland hardwood forests* category, the quadratic model was the best model (Figure 10c), but its W_i (0.414) was only marginally higher than that of the null model (0.320) and its adjusted R^2 value indicated that it explained only about 1% of the variation in the VSD. For the *Vegetated non-forested wetlands* category, the null model was the best model (Figure 10d).

Table 3: Akaike information criterion (AIC) model selection results for vertical structural diversity (VSD) as a function of time since fire (TSF) using linear models fit via least squares minimization. Bold indicates the best model based on the lowest AIC score (AIC_{min}) among the candidate models in each land use/land cover category, $\Delta_i = AIC_i - AIC_{min}$, and W_i is the Akaike weight for model i [see Johnson and Omland (2004) for formula to calculate W_i].

	Parameters	F (df)	p-value	Adjusted R^2	AIC	Δ_i	W_i
Herbaceous upland non-forested							
Quadratic	4	3.35 (2,163)	0.038	0.028	**806.47**	0	0.670
Null	2	NA	NA	NA	809.16	2.68	0.175
Linear	3	1.74 (1,164)	0.190	0.004	809.41	2.94	0.154
Shrub and brushland							
Linear	3	4.72 (1,57)	0.034	0.060	**257.47**	0	0.596
Quadratic	4	2.45 (2,56)	0.096	0.048	259.22	1.75	0.249
Null	2	NA	NA	NA	260.16	2.69	0.155
Wetland hardwood forests							
Quadratic	4	2.44 (2,254)	0.089	0.011	**1235.58**	0	0.414
Linear	3	2.37 (1,255)	0.125	0.005	1236.10	0.51	0.320
Null	2	NA	NA	NA	1236.48	0.89	0.265
Vegetated non-forested wetlands							
Null	2	NA	NA	NA	**330.77**	0	0.422
Linear	3	1.93 (1,59)	0.170	0.015	330.80	0.03	0.415
Quadratic	4	1.02 (2,58)	0.369	0.001	332.67	1.90	0.163

a) Herbaceous upland non-forested (*n* = 166)

VSD = 4.336 + 0.244*TSF - 0.008*TSF^2
(*p* = 0.038, Adjusted R^2 = 0.028)

c) Wetland hardwood forests (*n* = 257)

VSD = 10.883 - 0.119*TSF + 0.005*TSF^2
(*p* = 0.089, Adjusted R^2 = 0.011)

b) Shrub and brushland (*n* = 59)

VSD = 8.373 - 0.072*TSF
(*p* = 0.034, Adjusted R^2 = 0.060)

d) Vegetated non-forested wetlands (*n* = 61)

VSD = 6.942
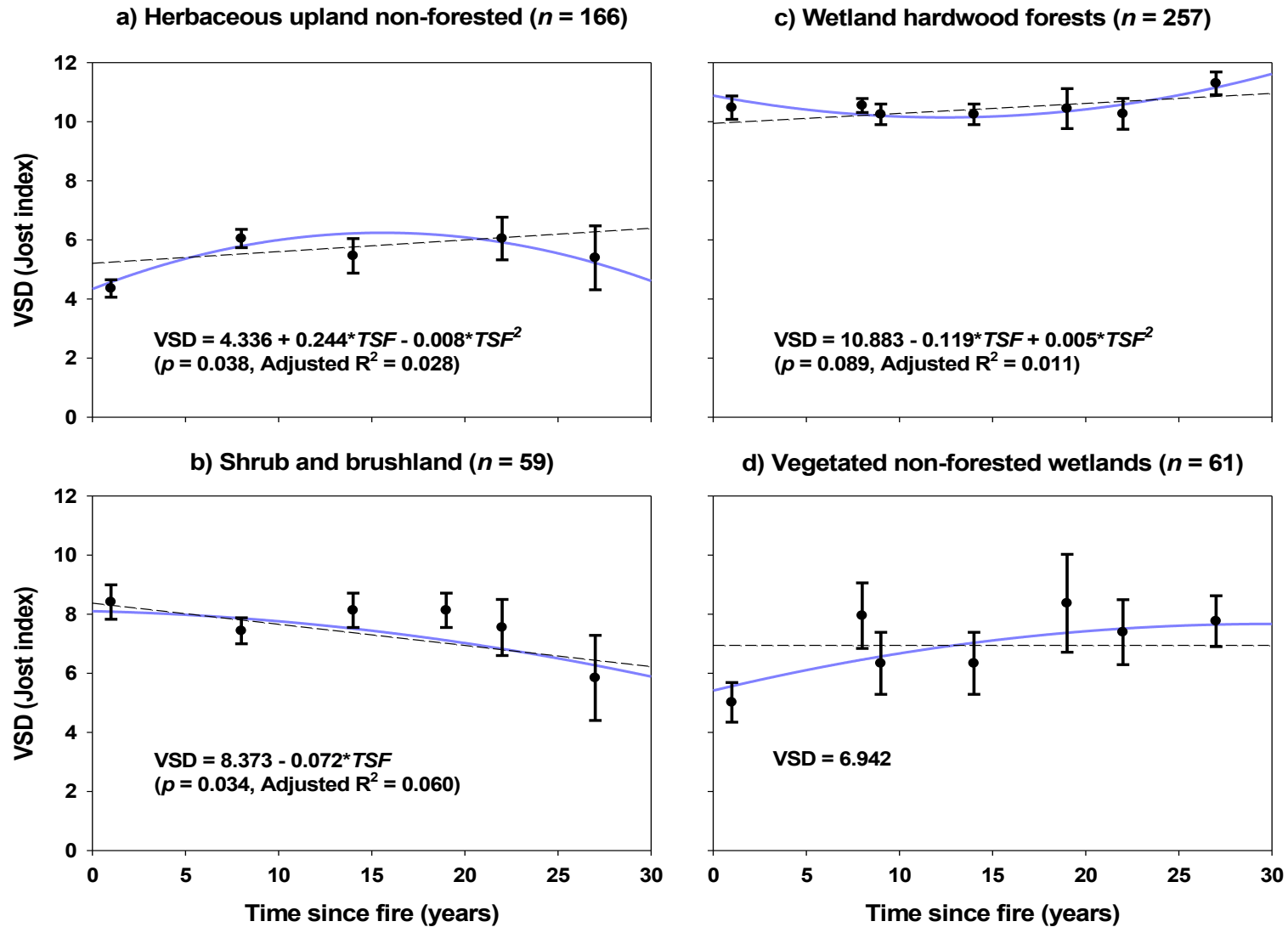
Figure 10: Plots of vertical structural diversity (VSD) as a function of time since fire (TSF). Solid line is quadratic model, dashed line is linear or null model, and equation indicates best model. Error bars are ± 1 SE of mean VSD.

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When fire frequency was considered in addition to TSF for the *Herbaceous upland non-forested* LULC category, the model with linear and quadratic terms for both frequency and TSF, as well as the interactions between these terms, was the best model (Table 4). Based on the AIC scores calculated for all of the models, the Aikaike weight for the best model ($W_i = 0.738$) was substantially higher than that of the other models and indicated that there was a probability of almost 75% that it was the best model among the candidate set of models for the observed data. Using this model, a response surface was plotted depicting the effects of both TSF and fire frequency on VSD in *Herbaceous upland non-forested* vegetation patches (Figure 11).

Table 4: Aikaike information criterion (AIC) model selection results for vertical structural diversity (VSD) as a function of time since fire (*TSF*) and/or fire frequency (*Freq*) for the *Herbaceous upland non-forested* category. All models listed are significant ($p < 0.001$). The '*' symbol in a model equation indicates the presence of both additive and interactive terms, and *K* is the number of estimable parameters in the model. Bold indicates the best model based on the lowest AIC score (AIC_{min}) among the candidate models, $\Delta_i = AIC_i - AIC_{min}$, and W_i is the Aikaike weight for model *i* [see Johnson and Omland (2004) for formula to calculate W_i].

Model	K	F (df)	Adj. R^2	AIC	Δ_i	W_i
$VSD = TSF*Freq + TSF^2*Freq^2$	**8**	**16.89 (6,1393)**	**0.064**	**6312.46**	**0.00**	**0.738**
$VSD = TSF + Freq + TSF^2 + Freq^2$	6	23.50 (4,1395)	0.060	6315.46	2.99	0.165
$VSD = TSF*Freq$	5	29.81 (3,1396)	0.058	6317.83	5.37	0.050
$VSD = TSF + Freq$	4	43.59 (2,1397)	0.057	6318.00	5.54	0.046
$VSD = TSF$	3	70.28 (1,1398)	0.047	6332.08	19.62	0.000
$VSD = TSF + TSF^2$	4	35.99 (2,1397)	0.048	6332.42	19.95	0.000
$VSD = Freq + Freq^2$	4	32.33 (2,1397)	0.043	6339.41	26.95	0.000
$VSD = Freq$	3	53.50 (1,1398)	0.036	6348.18	35.71	0.000
Null model	2	NA	NA	6398.76	86.29	0.000
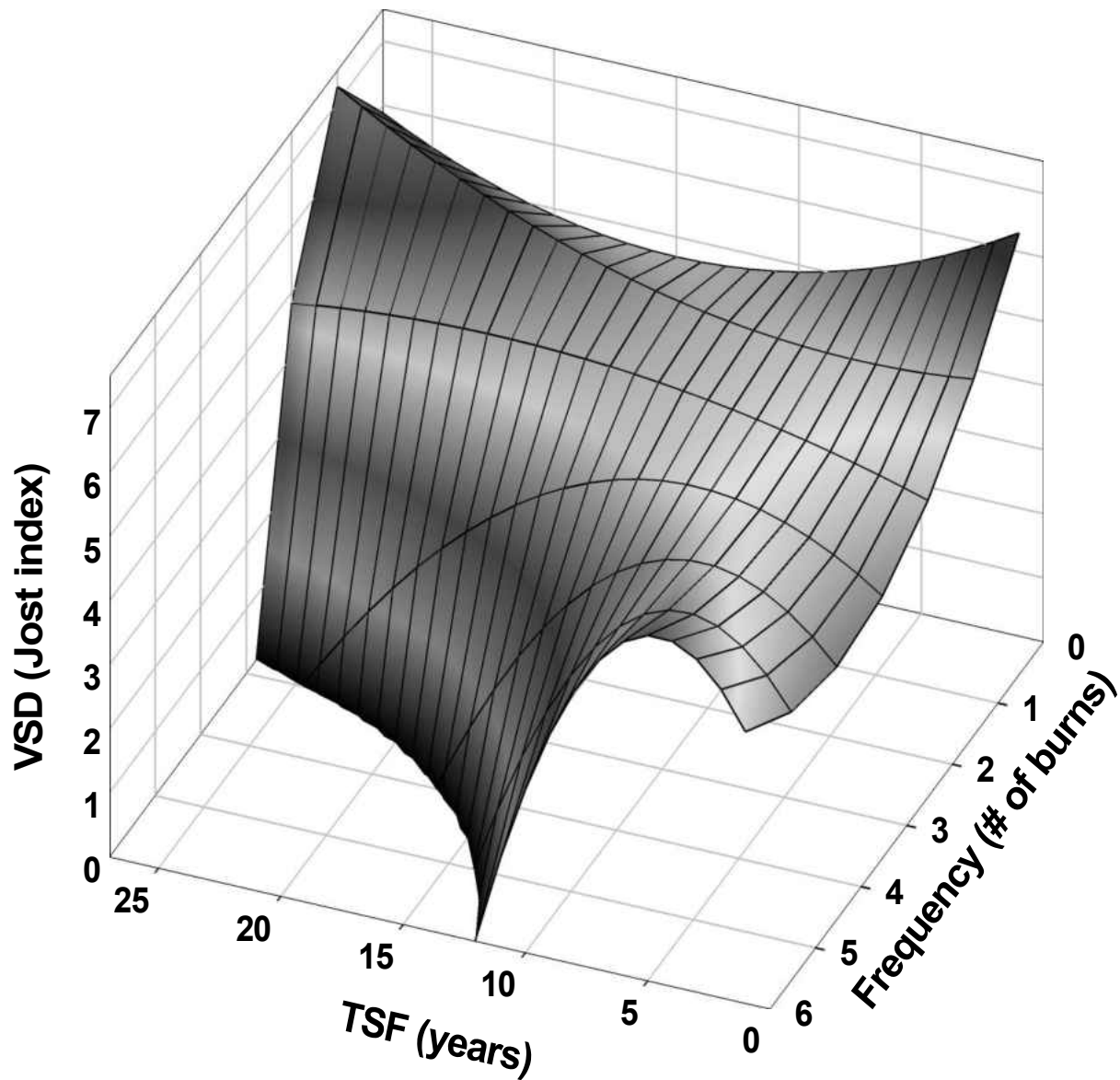
Figure 11: Vertical structural diversity (VSD) of vegetation patches classified as *Herbaceous upland non-forested* as a function of both time since fire (TSF) and fire frequency. The mesh surface was fitted using the double quadratic model ($VSD = TSF*Freq + TSF^2*Freq^2$) that was identified as the best model via the Aikaike information criterion (AIC) model selection procedure (see Table 4).

CHAPTER 4: DISCUSSION

In the first part of this study, vertical profiles generated from discrete-return lidar data were used to detect differences in the vertical structure of vegetation in an oak scrub landscape based on TSF. For the dominant LULC category (*Herbaceous upland non-forested*), which comprised nearly two-thirds of the study area, the pairwise NPMANOVA comparisons revealed several significant differences between TSF groups (Table 2). While all of the significant differences occurred between vertical profiles whose TSF values were seven or more years apart, not all pairwise comparisons of profiles separated by more than seven years were significantly different. In particular, the profiles in the TSF = 27 group were not significantly different from that of any other TSF group. This may have been attributable to the relatively low number of vegetation patches ($n = 9$, which was almost half that of the next smallest group) and/or the high amount of variation among the vertical profiles in the TSF = 27 group. Visual inspection of the graphs of the vertical profiles (Figure 8) suggests that the greatest differences in vertical structure in the *Herbaceous upland non-forested* LULC category occur within the first eight years after fire. These results agree with previous research documenting changes in the vertical structure of oak scrub vegetation over different values of TSF (Schmalzer and Hinkle 1987, 1992).

The results of the pairwise comparisons of vertical profiles provide support for Holling's Extended Keystone Hypothesis, which predicts that disturbance generates discrete structural patterns at the meso-scale in terrestrial ecosystems (Holling 1992). The vegetation patches

analyzed in this study ranged in size from 0.06 m^2 to 1.89 km^2, with an average patch size of

approximately 0.02 km^2. These patch sizes are, therefore, squarely in the meso-scale range of the

spatial scales defined by Holling (1992). It is also interesting to note that the range of vegetation

patch sizes in the study area also falls within that identified by White and Pickett (1985), 10^{-4} to

10^6 m^2, as being the most common range of spatial scales at which disturbance dynamics occur.

Furthermore, as predicted by the EKH, fire disturbance appears to have segregated the patterns

of vertical structure into a relatively small number of discrete categories. The vertical profiles

belonging to the TSF = 1 group are clearly distinct from those belonging to groups later in the

sequence of recovery from fire (with the exception of TSF = 27, as discussed earlier). Similarly,

the profiles in the TSF = 8 group are distinct from those that occur both earlier and later in the

post-fire sequence (see Table 2 and Figure 8).

The results of this study also provide some support for the Intermediate Disturbance

Hypothesis as it relates to VSD. As noted earlier, the IDH predicts that diversity will exhibit a

unimodal response as the time since disturbance increases (Connell 1978). Thus, if the VSD in

the systems considered in this study responded as predicted by the IDH, then the quadratic model

would be the best of the models evaluated through the AIC model selection process. This was

true for the dominant LULC category, *Herbaceous upland non-forested*, where the quadratic

model was both statistically significant and had a model weight that was almost four times

higher than that of the next-best model, the null model (Table 3, Figure 10a). While the quadratic

model was the best model for this LULC category, however, it explained less than 3% of the

total variation in VSD. When fire frequency was considered in addition to TSF, the best model

was the model that was quadratic in both the TSF and frequency terms (Table 4). This model was

highly significant, but it still explained only about 6.4% of the total variation in VSD. Based on

the response surface that was fit using this model, VSD appears to respond in a complex manner

when both TSF and fire frequency are considered (Figure 11). At higher frequencies of fire (i.e.,

3 or more burns), VSD exhibits the unimodal response to TSF predicted by the IDH. At the

lowest frequencies, on the other hand, VSD responds in the opposite manner (i.e., an initial

decline in VSD followed by an increase with greater values of TSF). This is consistent with other

research on Florida scrub systems indicating that relatively frequent fire is necessary to maintain

an open overstory, which in turn permits the existence of understory vegetation (Schmalzer and

Hinkle 1987, Menges 1999). The absence of frequent fires allows a closed canopy to develop,

thereby causing a decline in the density of understory vegetation and a lower level of VSD

(Beckage and Stout 2000).

For the other three LULC categories considered in this study, the quadratic model

relating VSD to TSF was either not significant and/or not the best model among the models

considered (Table 3). The best-fitting curve for the *Wetland hardwood forests* category was a U-

shaped quadratic response (Figure 10c), which is the opposite of the response predicted by the

IDH. Also, this model was not statistically significant and had only a marginally higher

probability of being the correct model ($W_i = 0.41$) than the next-best model, the null model ($W_i = 0.32$). For the *Shrub and brushland* and *Vegetated non-forested wetlands* LULC categories, the

linear and null models were, respectively, the best models. The linear model for the *Shrub and

brushland* category exhibited a negative, statistically significant relationship between TSF and

VSD (Figure 10b). Although the calculated Akaike weights indicate that this model had over

twice the probability of being the correct model than the quadratic model ($W_i = 0.60$ vs. $W_i =$

0.25), its adjusted R^2 value was only 0.06. Finally, the linear model had almost the same Akaike weight ($W_i = 0.41$) as the null model ($W_i = 0.42$) for the *Vegetated non-forested wetlands* category, but the linear model was not significant and it explained only about 1.5% of the total variation in VSD.

For the two hydric systems included in this study (*Wetland hardwood forests* and *Vegetated non-forested wetlands*), it was not particularly surprising that VSD failed to exhibit the unimodal response to TSF predicted by the IDH. Wetland hardwood hammocks rarely burn due to their lack of herbaceous cover and highly saturated soils (FNAI and FDNR 1990), which may explain the relatively high levels of VSD present at all values of TSF for this LULC category (Figure 10c). Non-forested wetland prairies and marshes, on the other hand, rely on fire every 2 – 4 years to prevent the invasion of woody vegetation (FNAI and FDNR 1990). The pattern of increased VSD at the highest TSF values for the *Vegetated non-forested wetlands* category (Figure 10d) may thus reflect the establishment of woody species in the prolonged absence of fire. Somewhat more surprising was the result that the linear model was a better model than the quadratic model for the *Shrub and brushland* category. Excluding the higher-than-expected VSD for the TSF = 1 patches, however, the VSD values for the remaining TSF groups appear to follow the unimodal pattern predicted by the IDH (Figure 10b).

While the quadratic models for the *Herbaceous upland non-forested* category (both those that include and do not include fire frequency) and the linear model for the *Shrub and brushland* category were significant, each of these models explained a relatively low amount of the total variation in VSD. Furthermore, as evidenced by the relatively wide error bars in Figures 10a and 10b, there is a considerable amount of variation in the VSD within a given TSF class for these

LULC categories. At least two factors might account for this high variability in VSD. First, forest ecologists have long realized that variation in environmental factors at the patch level (e.g., microclimate and resource availability) may affect diversity in concert with disturbance (Auclair and Goff 1971, Denslow 1980). In recognition of this, Huston (1979) expanded the basic IDH model to incorporate the possibility of variable population growth rates for competing species. Since site quality is presumed to affect growth rates, this model thus implicitly incorporates the effects of external environmental influences on diversity (Roberts and Gilliam 1995). At least some portion of the high variation in VSD may, therefore, be attributable to differences among the site qualities of the vegetation patches comprising each combination of LULC category and TSF value. Consequently, these exogenous environmental variables would have to be measured and incorporated into the models to improve the fit of the diversity-disturbance relationships.

Second, in the conclusion to his paper on the IDH, Connell (1978) emphasized that the species that comprise disturbance-prone ecosystems have often evolved adaptations to natural disturbances over extremely long periods of time, and that they may therefore respond in a qualitatively different manner to anthropogenic disturbances to which they aren't adapted. Thus, how well the diversity-disturbance relationship of a system follows that predicted by the IDH may depend on how well that system's current disturbance regime (i.e., the frequencies, magnitudes, and spatiotemporal patterns of disturbance) mimics that of its natural disturbance regime (Denslow 1980). As discussed in Duncan et al. (2009), some key aspects of the managed fire regime in the study area differ substantially from that of the historic disturbance regime. For example, natural fires in Florida oak scrub landscapes tend to occur during the growing season

(i.e., spring and summer), while the majority of the prescribed burns in the study area were conducted during the dormant season (i.e., fall and winter). Also, naturally occurring fires exhibit intra-seasonal variation in intensity as fuel loads become saturated due to heavy rainfall in the later part of the growing season. Finally, anthropogenic fire breaks and other restrictions on burning in the study area have produced burned patches with strongly linear features (Figure 3), as opposed to the fuzzier ecotones generated by more natural boundaries to the spread of fire (Boughton et al. 2006, Duncan et al. 2009). Together, these differences represent potentially major departures from the historic disturbance regime in the study area, and may thus profoundly influence the diversity-disturbance relationships observed.

The results of this research have several potentially important implications for studying and managing forest and shrubland ecosystems. Smith (1973) argued that the "heterogeneity of vertical foliage distribution is, in itself, a major parameter of the biotic environment…and must be quantified." The methodology developed in this study to create and compare vertical profiles and the results of these comparisons indicate that discrete-return lidar data can accurately quantify the vertical structure of a variety of vegetation types, in various states of recovery from disturbance, and at spatial scales larger than those previously possible. While methods to characterize vertical profiles have existed for almost 50 years since the pioneering work of MacArthur and MacArthur (1961), these studies have been quite limited in spatial scale. For example, Aber's (1979) seminal comparison of vertical profiles from different successional states was based on data collected from 13 plots that were 50- x 100-m in size. More recent studies have employed modern field-based methods to create vertical profiles for approximately 14.5 ha (Van Pelt and Franklin 2000) and 1.3 ha (Herrera-Montes and Brokaw 2010) of forest.

By comparison, with the methodology developed in this study, discrete-return lidar data were used to create vertical profiles for more than 500 vegetation patches over an area of approximately 10 km^2 (1000 ha).

Furthermore, the results of this research suggest that vertical profiles derived from discrete-return lidar can be a powerful tool to assist forest ecologists and other natural resource managers in their ongoing efforts to maintain and restore biodiversity. Since MacArthur and MacArthur's (1961) study correlating bird species diversity with foliage height diversity, scores of studies have found significant positive correlations between habitat heterogeneity and animal species diversity (Tews et al. 2004). The present study has demonstrated the ability of discrete-return lidar to quantify one important aspect of habitat heterogeneity—vertical structural diversity—on a landscape scale, and thus raises the possibility that such information might be used for conservation site selection and monitoring. For example, managers could use the techniques developed in this study to compare the vertical profiles and structural diversity indices of managed forest plots to those from comparable "reference sites" in unmanaged forests (Roberts and Gilliam 1995). Finally, vertical profiles might be used to infer the time-since-last disturbance status of vegetation patches in the absence of historical records of an ecosystem's disturbance history (Angelo et al. 2010).

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