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The Effects Of Urbanization On Cypress (taxodium Distichum) In Central Florida

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THE EFFECTS OF URBANIZATION ON CYPRESS (*TAXODIUM DISTICHUM*) IN CENTRAL FLORIDA

by

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ABSTRACT

Urbanization is accelerating in the United States and is contributing to fragmentation of natural habitats, causing changes in species composition and declines in native species. Human population growth in Orlando is typical of growth in the southeastern United States and throughout the range of cypress (*Taxodium distichum*). Orlando has numerous isolated cypress wetlands, called cypress domes, and many remain among the current urbanized area. This makes Orlando ideal to study the effects of urbanization on cypress domes. Specifically, I tested how urbanization and its effects on fragmentation, hydrology, and fire regime) affected (a) the numbers and spatial pattern of cypress domes in central Florida and (b) the recruitment of cypress within cypress domes. Analysis of historical loss found over 3,000 cypress domes identified in images from1984, of which 26% were lost or degraded (i.e., no longer cypress-dominated) by 2004. Due to changed land use, many remaining cypress domes, formerly surrounded by natural lands, have become surrounded by urban lands causing spatial clustering and homogenization. Surprisingly, I found that both natural and urban cypress domes showed lower recruitment than agricultural cypress domes, where the natural fire regime has not been altered. The probability of cypress recruitment in cypress domes urbanized for more than 20 years is very low. Previous to that, cypress tends to recruit on the edge of cypress domes where there is less competition and hydrological conditions are more favorable. I estimate that only ~50% of the current cypress domes are recruiting and the existence of those wetlands are tied to the lifespan of the current adults. By 2104, I estimate that ~89% of the cypress domes currently recruiting will fail to recruit. I believe that reducing urban sprawl and restoring the natural fire

regime to natural cypress domes will mitigate the current fate of cypress domes. Without this, cypress in isolated wetlands in central Florida, and providing Orlando urbanization is typical, throughout urbanized areas of the range, could be at risk. Cypress in urban areas will be then relegated to riparian zones and with unknown consequences for the species that utilize the former cypress dome habitat.

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CHAPTER 1: INTRODUCTION

For the first time in human history, more people live in urban areas than rural areas worldwide (UNFPA 2007). Nearly 84% of the U.S. population lives in urban areas currently and that number is expected to rise (U.S. Census Bureau 2000, 2010a). The conversion of land to urban use (urbanization) is one of the leading causes of species loss in the United States (Czech et al. 2000) and conversion of land to urban use is increasing at faster rates than lands are being preserved as parks or conservation areas (McKinney 2002). Urbanization has been shown to increase fragmentation of natural habitat, decrease native species diversity, and increase invasion of exotic species (Medley et al. 1995, Blair 1996, Pickett et al. 2001, McKinney 2002, 2004, 2006, D'Antonio and Meyerson 2002).

Human population growth in the southeastern U.S. has increased at faster rates than other areas of the country. For example, Florida's population has doubled in size every 20 years since 1900, causing a 3.5% increase annually (the nationwide average is 1.1%). Florida's population growth is estimated to reach 20.3 million people by the year 2020, leading to 1.05 million ha of additional urban land use area and consuming 7.5% of the total land area in Florida (Reynolds 2001).

The southeastern U.S. and especially Florida are home to numerous freshwater wetlands including isolated wetlands. Isolated wetlands are often smaller than riverine or coastal wetlands but are very numerous and typically sum to the greatest area among all wetland types in any given region (Semlitsch and Bodie 1998, van der Valk and Pederson 2003). Isolated wetlands also provide unique habitat for several species. Due to the lack of fish, amphibian species diversity has been found to be highest in isolated wetlands (Semlitsch and Bodie 1998). In addition, isolated wetlands also provide important habitat for waterfowl breeding and feeding (Leibowitz 2003). In this study, “isolated” refers to wetlands that are not often hydrologically connected but could have biotic connections during large rainfalls or by overland dispersal.

Protection of isolated wetlands has been at issue in recent years. The 2001 U.S. Supreme Court decision in the Solid Waste Agency of Northern Cook County (SWANCC) vs. U.S. Army Corps of Engineers (USACE) limited federal protection of “non-navigable, intrastate” waters, possibly leaving isolated wetlands unprotected from further destruction (Mank 2003; SWANCC v. U.S. Army Corps of Engineers). The Court found that federal protection is limited to navigable waters and non-navigable waters that have a “significant nexus” to navigable waters, such as those adjacent to navigable waters. Recognition of biotic connections, via dispersal of organisms, could be considered as a “significant nexus” and could help protect isolated wetlands.

Many of these isolated wetlands are cypress domes, which are dominated by cypress (*Taxodium distichum*) and called domes because of the dome shape caused from taller trees in the middle and shorter trees around the edge. I chose cypress domes as a model system to study the effects of urbanization on isolated wetlands in a rapidly urbanizing area. I chose cypress domes and the dominant vegetation cypress (*Taxodium distichum*) for this study because of three main reasons. First, there are numerous cypress domes and cypress trees readily available for sampling. Second, cypress is readily distinguishable on color infrared aerial photography making analysis possible across large spatial scales and through time. Lastly, cypress is a long-lived species in which adults were present prior to urbanization and juveniles have recruited since urbanization. This allows for evaluation of genetic differentiation between adults and juveniles to determine the effects of urbanization on the population genetics of the species.

Cypress

Cypress trees dominate forested wetlands of the southeastern U.S. and occur in both isolated wetlands (such as cypress domes) and riparian zones of rivers and streams. The native range of cypress includes 17 states throughout the southeastern U.S. (Figure 1). Cypress are a gymnosperm and monoecious. Cypress produce an average of about 16 seeds per cone (Faulkner and Toliver 1983) and good seed crops are produced about every 3-5 years (U.S. Department of Agriculture 1974, Brandt and Ewel 1989). A major vector of dispersal of cypress cones is via hydrochory (Middleton 2000) during temporary hydrological connections that occur with significant rainfalls. Seeds will remain viable for up to 30 months underwater but they will not germinate underwater. Germination requires saturated but not flooded conditions in order to germinate and seedlings must stay above water for the first year in order to survive (Demaree 1932). Adults can live to be several hundred years old if not logged (Burns and Honkala 1990).

Two varieties of cypress have been recognized: pond cypress, which is typically the dominant variety in cypress domes, and bald cypress, which is commonly found along flowing water systems. Bald cypress is morphologically different from pond cypress but the taxonomic difference between the two has been debated (Watson 1985, Brandt and Ewel 1989, Ewel 1995, Tsumura et al. 1999, Lickey and Walker 2002). I was most likely dealing with pond cypress but will, in general terms, often refer to *T. distichum* simply as cypress.

For cypress domes and the cypress trees that define them, urbanization can involve three major alterations: fragmentation, alterations to hydrology and alterations to fire regime. Each alteration is discussed below.

Fragmentation of a naturally-fragmented system works differently than in continuous habitats because entire patches of habitats and therefore entire populations of organisms can be removed. Fragmentation removes entire cypress domes from the landscape and should increase the dispersal distance for cypress. Thus, cypress gene flow should be reduced with increasing urbanization.

Isolated wetlands have naturally variable hydrology, filling up during significant rainfalls and drying during periods of less rainfall. Urban stormwater systems often divert incoming rainfall into retention areas to avoid flooding roads and buildings. Cypress domes that remain among urbanization may be used in stormwater systems as retention ponds (that permanently hold water), or may be drained to reduce flooding risk. The hydrology then becomes “polarized”, changing from variable to the two extremes of permanently flooded or completely drained. Polarized hydrology is likely to limit cypress germination. In addition, urban hydrological regimes limit the temporary water connections that contribute to dispersal of cypress during significant rainfall. Removal of temporary water connections is likely to limit dispersal and gene flow of cypress in urban areas causing recruitment to occur from adults within a site and not from other cypress domes. Because cypress trees can live to be several hundred years old, adult metapopulation genetic structure may represent conditions before Orlando’s recent urbanization. However, juvenile cypress should have less genetic variation than adults on-site because gene flow among cypress domes is now limited.

Cypress domes dry out frequently and occur within a naturally pyrogenic upland landscape and are therefore adapted to frequent fires. A natural fire regime is likely to prevent succession to bay swamps and prevent build up of organic matter (Penfound 1952, Casey and Ewel 2006). Fires are suppressed in urban areas in order to avoid risk to real estate. Reduced fire frequency in urban areas allows encroachment of woody vegetation that can out-compete cypress seedlings and allows sub-canopy shading of cypress seedlings (Ewel 1995). It is possible that fire may also increase cypress seed production (Ewel 1995). In the absence of fire, woody vegetation encroachment in cypress domes also causes succession into mixed-hardwood swamps and bayhead swamps (Wade et al. 1980, Casey and Ewel 2006).

I tested how urbanization (fragmentation, altered hydrology, and altered fire regime) affected (a) the numbers and spatial pattern of cypress domes in central Florida and (b) the recruitment of cypress within cypress domes. I attempted to test (c) gene flow of cypress among cypress domes but encountered difficulties in the assessment and was unable to evaluate this hypothesis. I then combined information from a & b into a Geographic Information System (GIS) model that uses historical changes and recruitment projections to predict future effects of urbanization on cypress domes in central Florida. My study will help guide management of remaining cypress domes for the effects of urbanization by investigating the cumulative effects of wetland loss and the value of biotic connectivity among wetlands.

CHAPTER 2: ISOLATED WETLAND LOSS AND DEGRADATION OVER TWO DECADES IN AN INCREASINGLY-URBANIZED LANDSCAPE

Introduction

The spatial distribution of modern human population growth has been heavily biased to urban areas, so that the majority of people now live in urban areas (UNFPA, 2007). For example, metropolitan populations in the U.S. increased 30% since 1990. Nearly 84% (>250 million people) of the US population lived in metropolitan areas in 2009 (U.S. Census Bureau 2000, 2010b). Rapid urban human population growth leads to thorough and widespread land-use changes and increasing demands on regional natural resources in both developing and developed countries (Jenerette and Potere 2010). Conversion of land to urban use (urbanization) is essentially permanent and increasing at faster rates than lands are being preserved as parks or conservation areas (McKinney 2002). Urbanization is one of the leading causes of species loss in the United States (Czech et al. 2000); it can decrease native species diversity directly by eliminating habitat (McDonald et al. 2008) and indirectly by increasing fragmentation and isolating natural habitat (McKinney 2002, 2006).

The southeastern United States has experienced greater population growth than other US regions and has many rapidly expanding urban areas (Figure 1). For example, the Orlando metropolitan area of central Florida gained over 850,000 people (a 70% increase) from 1990-2009. This growth is very similar to mean population growth (68%) of the major cities in the Southeast during the same time (Figure 1; U.S. Census Bureau 2000; 2010b). Thus, the Orlando metropolitan area is representative of typical urbanization patterns in the southeastern US and is an ideal location to evaluate the effects of urbanization.

Compared to regions in which wetlands were long since destroyed by extensive human land use (McCauley and Jenkins 2005), central Florida was developed relatively recently and includes numerous extant wetlands, many of which remain among current urbanization (Haag and Lee 2010). Urban wetlands provide valuable ecosystem services including flood water storage, sediment filtration, nutrient and pollutant removal, and ecological habitat (Xu et al. 2009, Haag and Lee 2010). However, increasing urban demands can alter urban wetlands and reduce their ability to provide such services. Thus, understanding the effects of urbanization on wetlands embedded in an urbanized landscape is essential to maintaining and improving the ecosystem services they provide and conserving their biodiversity.

Wetlands can be categorized as either hydrologically connected or hydrologically isolated, and this distinction is important in U.S. wetland protection laws. Isolated wetlands are not protected as fully as “navigable”, riverine wetlands (SWANCC v. U.S. Army Corps of Engineers 2001; Craig 2002). Both types of wetlands are important in urban landscapes but isolated wetlands are particularly susceptible to urbanization because they are located within a modified, upland matrix, whereas riverine areas are less often urbanized due to flooding risk. Isolated wetlands are often smaller than riverine or coastal wetlands but are very numerous, naturally fragmented, and typically sum to the greatest area among all wetland types in any given region (Semlitsch and Bodie 1998). Isolated wetlands also provide unique habitat for multiple species and are numerous in central Florida (Semlitsch and Bodie 1998, Leibowitz 2003, Herault and Thoen 2009, Haag and Lee 2010).

Many forested wetlands in the southeastern U.S. are dominated by cypress (*Taxodium distichum*) trees. This species has a distinct spectral appearance making them readily detectable in color infrared (CIR) images (Blazquez 1992a; 1992b). Two varieties of cypress (bald cypress and pond cypress) are recognized in the U.S. and I was most likely dealing with pond cypress, but I will generally refer here to *T. distichum* as cypress. Because urbanization in the southeastern U.S. has been rapid and recent, CIR images can be used to describe individual wetlands through decades and at spatial scales that would otherwise be challenging. For the Orlando metropolitan area, CIR photos are available beginning in 1984, making landscape-level analysis of cypress across a 20-year time period possible in this rapidly urbanizing landscape. Because Orlando is typical of urbanization in the southeastern US and the range of cypress encompasses much of that rapid urbanization (Figure 1), results obtained here may represent trends throughout much of the range for this currently common species, and thus for the isolated wetlands it dominates.

Isolated wetlands dominated by cypress are known as “cypress domes” because cypress trees are taller in the middle and shorter around the edge. Cypress domes (and riparian zones of rivers and streams also dominated by cypress) are important habitat for diverse other wetland species (Brandt and Ewel 1989, Ewel 1998, McKinney 2002). It is important to evaluate the effects of urbanization on wetland metapopulations and on wetland habitat quality for the variety of species that utilize cypress domes. This is possible using CIR photos because it is possible to distinguish cypress dome degradation (increase of non-cypress vegetation) from cypress dome destruction (loss of the entire wetland). Cypress domes are ideal for metapopulation and metacommunity studies because they are naturally discrete patches in which populations are likely connected by dispersal.

The purpose of this study was to quantify the effects of urbanization on cypress dome number, size and pattern across space and time, using Orlando, FL as a case study. I described changing land use and cypress dome numbers, sizes, and spatial distributions in different land use categories in the Orlando region in 1984 and 2004, during a period of rapid urbanization.

Methods

Detecting cypress domes

Color-infrared aerial photos from 1984 and 2004 and land cover data from 1990 and 2004 were acquired from St. John's River Water Management District for Orange and Seminole counties in the Orlando region of central Florida, USA (28°36'N, 81°18'W; Figure 2). In order to use the greatest time span possible, the oldest color infrared photographs (from 1984) were used. However, land cover from 1984 was unavailable so 1990 land cover data was substituted. A small portion (10%) of the study area was not included in the analysis because color-infrared aerial photos from 1984 were unavailable for those areas. Using ArcGIS v9.2 (ESRI 2006), all forested wetlands were exported from the total land cover database and overlain onto the aerial photos. Landcover data were manually corrected to match aerial photos by examination at a 1:12,000 scale; forested wetlands were removed, added, or modified as necessary to obtain an accurate coverage of cypress domes. Automated selection procedures were attempted but were found to lack sensitivity and results were inaccurate relative to manual processing. Polygons in close proximity to riverine habitats were removed so that only hydrologically isolated cypress domes were chosen for analyses.

Quantifying urbanization

In order to quantify the urbanization intensity of each cypress dome, I categorized land cover surrounding each cypress dome. I first created a demarcated zone (called a “buffer”) in ArcGIS v.9.2 (ESRI 2006) around each cypress dome equal to the average nearest neighbor distance (263 m). Based on descriptions provided with the land cover data layer, five potential land cover categories were identified: natural, agriculture, low urban, medium urban, or high urban. For example, land cover descriptions such as golf courses, recreation, and low density housing were classified as low urban and descriptions such as crops, cattle operations, and citrus groves were classified as agricultural. Principal Component Analysis (PCA) was used to reduce the proportions of each of the 5 land cover categories within the buffer to two multivariate axes. Each axis was then plotted against each of the 5 original land cover proportions. Each graph was evaluated and a range of axis values that represented that category was estimated, based on where the majority of points fell on the graph. For example, when each axis was plotted against the agricultural proportions in each buffer, the majority of points that were high in agriculture were less than -0.5 for axis 1 and between -1 and 1 on axis 2. The ranges obtained from the graphs were used to assign each cypress dome into one of the 5 categories. Canonical Discriminant Analysis was used to test the categories and 92.4% of the cases were classified correctly, which I considered sufficient to represent the urbanization gradient. To ensure the accuracy of dome categorization between years, I also evaluated differences in assignment between years for all cypress domes. Any cypress dome identified as becoming less urban (an unlikely event) during the 20-year time period was re-evaluated to verify its urbanization category. Only ~5% of the 1984 polygons were re-categorized by this data-quality processing.

Urbanization effects on wetland loss and local degradation

Cypress domes that were present in 1984 but judged as absent in 2004 were evaluated further in GIS to determine if the loss was due to habitat destruction or habitat degradation. Habitat destruction was apparent because vegetation had been removed and the wetland was destroyed (e.g., replaced by roads or buildings). Habitat degradation was assumed in those cypress domes that existed in 1984 but no longer had the spectral signature of cypress in 2004 though the wetland still existed. In most of these cases, other vegetation had encroached so that the cypress trees could no longer be distinguished from the upland vegetation. Losses by destruction or degradation were recorded separately.

Urbanization effects on cypress dome pattern

Changes in cypress dome spatial patterns were calculated by evaluating statistical descriptors spatial position and size. I used ArcGIS v9.3 (ESRI 2009) to calculate three measures of cypress dome spatial pattern by urbanization category in 1984 and 2004. I used Ripley’s K to evaluate spatial clustering of dome locations. Ripley's K evaluates spatial clustering of locations, relative to Monte Carlo randomizations, such that an observed Ripley's K value greater than expected indicates spatial clustering of cypress domes. Ripley’s K values were calculated for each urbanization category in 1984 and 2004 with 20 distance classes and 99 permutations representing approximately a 99% confidence interval. Significant clustering was indicated by an observed Ripley's K value greater than the upper 99% confidence limit of the expected Ripley's K.

Anselin Local Moran's I values for each urbanization category in 1984 and 2004 were calculated to estimate spatial autocorrelation of cypress dome size (area). Finally, a Spatial Isolation index was calculated for each cypress dome by drawing a buffer equal to twice the nearest neighbor distance of the 1984 cypress domes (490m) and using Hawth's Tools (Beyer 2004) to count the number of other cypress domes present within each buffer in both 1984 and in 2004. One way analysis of variance (ANOVA) and independent samples t-tests were used to evaluate significant differences in Local Moran's I values, cypress dome areas, and Spatial Isolation index values across urbanization levels and years.

Results

Numbers and Area

A total of 3,393 cypress domes (6,363 ha) were detected from the 1984 aerial photos. Of these, 92% were categorized as natural or agricultural (Figure 2, Table 1). By 2004, the total number of cypress domes dropped to 2,498 (4,677 ha), for a loss of 26% in number and area. Nearly half of the natural cypress domes were destroyed, degraded, or re-categorized because surrounding land use had changed (Figure 2, Table 1). The number of cypress domes categorized as urban increased substantially from 1984 to 2004, and within the urban subcategories, low-urban cypress domes increased three-fold, medium-urban cypress domes increased by 50%, and high-urban cypress domes increased two-fold (Table 1). Similarly, from 1984 to 2004, cypress dome size (area) was significantly reduced in natural and agricultural categories and significantly increased in urban categories (Table 1). This was a result of increased urban land use surrounding the remaining cypress domes in 2004.

Overall, almost four times more cypress domes were lost to habitat degradation than were lost to habitat destruction and this general pattern was true for all land use categories (Table 2). Surprisingly, the proportion of cypress domes that degraded in natural lands was twice the proportion that disappeared and degradation exceeded the rate of conversion to urban land use. Degradation also affected nearly 25% of the 1984 agricultural cypress domes but cypress dome degradation was less common in agricultural lands than in natural lands.

Many cypress domes that were formerly surrounded by natural lands became surrounded by low-urban land use. This conversion occurred mainly at the periphery of Orlando, especially in the southeast portion of the study area (Figure 2). In contrast, most of the extant agricultural cypress domes that changed land use categories were re-categorized to natural domes. These were mainly in large tracts of land that were taken out of agricultural production and put into management as natural lands. The cypress domes that were classified as urban in 1984 tended to become more urban or disappear/degrade. No cypress dome classified as urban in 1984 was converted back to a natural or agricultural category by 2004 (Table 2).

Spatial Pattern

Cypress domes were significantly clustered in both 1984 and became more so by 2004 at most, as indicated by Ripley's K values (Figure 3). Low-urban cypress domes showed increased clustering from 1984 to 2004. In 1984, both low-urban and medium-urban cypress domes were not significantly clustered at large distances (10,000 – 12,000 m) but by 2004 both categories were significantly clustered at all distances (Figure 3). Similarly, the spatial isolation index showed significant differences among groups (1984: $p<0.01$, F=60.55; 2004: $p<0.01$, F=22.59) and low-urban cypress domes were less clustered in 1984, significantly grouping with other urban categories ($p<0.01$), but by 2004 low-urban cypress domes were more clustered, significantly grouping with natural and agricultural domes ($p<0.01$; Figure 4). It is important to note that increased clustering was not caused by cypress domes being created or moved, but was due to the conversion of surrounding land cover that caused cypress domes to be re-categorized.

In 1984, agricultural cypress dome sizes were significantly more heterogeneous in space (i.e. small cypress domes were intermixed with larger cypress domes) than natural or urban domes (local Moran's I; p=0.002, F=6.455). By 2004, this effect was largely gone (p=0.105, F=2.253) and sizes were more homogeneous (i.e. small cypress domes were now nearer other small cypress domes and large cypress domes were now nearer other large cypress domes) in all land use categories. Across all categories, cypress domes that were lost from 1984 to 2004 were significantly smaller (p=0.04, F=4.209) than cypress domes that remained. In 1984, urban cypress domes were significantly larger than agricultural and natural cypress domes ($p< 0.001$, F=15.81) but by 2004, this heterogeneity was largely lost (p= 0.079, F=2.545). Large, urban cypress domes and small, agricultural and natural cypress domes were both lost, causing all categories to converge on an average wetland size of ~ 1 ha (Figure 5).

Discussion

Although urbanization began in the Orlando metropolitan region in the 1960’s (Gladstone 1998), 92% of the cypress domes remaining in the two counties encompassing the core Orlando metropolitan region were still categorized as natural or agricultural in 1984. However, half of the natural cypress domes and 30% of the agricultural cypress domes were lost, degraded or re-categorized by 2004, despite legal protection of these habitats (FDEP 2007).

During the study period, a number of conservation and wetland protection programs (e.g., Florida Forever, Preservation 2000; FDEP, 2007) were established to preserve natural lands or convert lands into conservation areas. This effort is demonstrated in the re-categorization of 140 wetlands (230 ha) of cypress domes from agricultural to natural. However, these efforts did not equal the urbanization that has surrounded and affected many cypress domes (Table 1). Urbanization appears to be widespread and essentially permanent, with no cypress domes categorized as urban in 1984 moving to a more natural category by 2004.

During the twenty years, one fifth of cypress domes were degraded, meaning that the wetland remained but was so overgrown by other vegetation that cypress trees were no longer detected on aerial photos. Beyond potential effects on cypress population structure and habitat quality for other wetland species, degradation alone may cause the habitat to lose protection under wetland regulations (University of Florida/ IFAS Extension 2006) making subsequent, legally-permitted destruction of the wetland more probable. Degradation is likely due to urbanization-driven alterations in hydrology and/or fire regime in the cypress dome and surrounding matrix. Urbanization alters hydrology to avoid flooded homes. The changes to drainage patterns can “polarize” the hydrology of isolated wetlands that naturally have variable hydrology to become either permanent retention ponds or drained wetlands. Both hydrological regimes reduce local recruitment of cypress by limiting both germination and seedling survivorship. Cypress germination requires saturated but not flooded conditions and seedlings must not be immersed for the first year in order to survive (Demaree 1932). Urbanization also reduces fire frequency because fires are immediately suppressed, which is an especially pronounced change from the natural fire regime that prevents succession of cypress domes into hardwood swaps (Penfound 1952, Casey and Ewel 2006). Fire suppression allows for encroachment of woody vegetation, potentially reducing possible fire-induced increases in cypress seed production and increasing sub-canopy shading of cypress seedlings (Ewel 1995). I hypothesize that these processes may ultimately reduce recruitment in isolated cypress populations in urbanized areas and, if Orlando has typical urbanization, this may occur throughout the cypress range.

Changes in spatial patterns from 1984 to 2004 have likely affected metapopulation-level processes for cypress, such as dispersal and gene flow. Land cover conversions have caused cypress domes surrounded by natural lands in 1984 to be surrounded by low- or medium-urban land use in 2004. Urbanization should fragment remaining cypress populations through both the loss of entire cypress domes and loss of hydrological connections between wetlands (Fahrig 2003). In natural landscapes, hydrological connections may occur after significant rainfalls and can be an important means of biotic connectivity for several species, especially plants with floating seeds (Kirchner et al. 2003). Hydrological connections disperse cypress seeds among cypress domes in natural landscapes (Middleton 2000). Altered hydrology as a result of ditches, roads, and increased impermeable surfaces in urban landscapes limit hydrological connections among cypress domes. Thus, urbanized areas throughout the range of cypress should have fewer connections among fewer cypress domes, leading to less dispersal and gene flow and a breakdown of the metapopulation structure. Recruitment within a population, rather than among cypress domes, should then dominate and lead to higher levels of inbreeding in juveniles when compared to pre-urbanization adults. The ultimate consequence of widespread urbanization for cypress domes will then be limited dispersal and gene flow, increased inbreeding of juveniles, and reduced germination and seedling survival in extant populations throughout the southeastern U.S. range of cypress.

Cypress domes became more homogeneous in size across the greater Orlando region during the 20-year study period. Land use changes appear to have caused the loss of small cypress domes in natural and agricultural areas. Small cypress domes have a greater edge:area ratio and are more susceptible to degradation due to encroachment by woody vegetation in the absence of fire. In the two decades studied, smaller cypress domes continued to be lost in natural areas and the remaining larger cypress domes were lost in urban areas likely due to both hydrological and fire frequency changes. The result was the average size of cypress domes across the region became more similar, leaving only medium-sized domes around 1 ha (Figure 4). Loss of small populations, while seemingly unimportant demographically, can lead to a decrease in overall genetic diversity because some small populations can be particularly valuable genetically, potentially containing rare alleles (Godt et al. 1995, Fleishman et al. 2001). In addition, small wetlands often lack predatory fish and alligators and can support populations of species not found in other, larger wetlands, including some invertebrates, plants, amphibians, and waterbirds (Semlitsch and Bodie 1998, Herault and Thoen 2009, Ma et al. 2009). Small, isolated wetlands also contribute to high landscape-level species diversity because they differ greatly from larger wetlands and from one another (Scheffer et al. 2006). Considering cypress wetlands provide habitat for a variety of plants, birds, mammals, reptiles, amphibians and invertebrates throughout its range (Brandt and Ewel 1989, Ewel 1998), loss of heterogeneity can affect a variety of species. Species-area relationships and island biogeography theory (MacArthur and Wilson 1967) suggest that large wetlands are also important to maintenance of regional biodiversity. Oertli et al. (2002) measured diversity in 80 similarly sized ponds and found that while some species were most frequent in small wetlands and some species were more numerous in large wetlands, none of the 64 examined taxa preferred medium-sized ponds. Homogenized wetland size during the course of 20 years' urbanization in central Florida likely contributed to a decrease in both species-level genetic diversity and regional biodiversity in remaining cypress domes. Similar range-wide urbanization effects could lead to detrimental consequences for cypress domes and the species that utilize the habitat.

Our results differ from other studies examining urbanization effects on patch pattern. Previous studies examined “continuous” systems (forests and deserts) in which urbanization divided large areas into smaller patches, increased patch numbers, and decreased patch sizes (Medley et al. 1995, Luck and Wu 2002). Cypress domes are naturally fragmented and urbanization removed or degraded entire cypress domes, leading to fewer patches with increased dispersal distances. However, other studies (McKinney 2006, Blair and Johnson 2008) found similar effects in which urbanization also removed some small and some large cypress domes, leaving medium-sized patches and contributing to a loss of heterogeneity.

Providing Orlando urbanization is typical, our results suggest that *Taxodium distichum* in isolated wetlands could be at risk in urban areas throughout the range. During the 20-year study period, one-quarter of the cypress domes were either destroyed or degraded and many remaining wetlands were urbanized. If this trend continues range wide, natural populations of *T. distichum* may persist only in riparian zones and species that depend on cypress dome habitats will likely be affected. The *T. distichum* populations in extant isolated wetlands will likely show further loss and degradation and I hypothesize will show reduced gene flow, decreased genetic diversity, and lower recruitment. Also, the wetlands may harbor lower regional species diversity and increased invasive species as urbanization continues to threaten wetland habitats (Duguay et al. 2006, Biamonte et al. 2011) . Despite the current commonality of cypress throughout its range and the fact these wetlands are partially protected by legislation, cypress in isolated wetlands of urban areas may become rare.

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CHAPTER 3: THE EFFECT OF URBANIZATION ON RECRUITMENT OF CYPRESS (*TAXODIUM DISTICHUM*) IN ISOLATED WETLANDS IN CENTRAL FLORIDA

Introduction

Conversion of land to urban use (urbanization) is one of the leading causes of native species diversity loss because it permanently destroys natural habitats, fragments remaining natural systems, and causes biotic homogenization (McKinney 2002, McDonald et al. 2008). Urban areas are expanding globally because human population growth in urban areas is increasing at rapid rates worldwide (UNFPA 2007). Nearly 84% of the U.S. population now lives in metropolitan areas (U.S. Census Bureau 2000; 2010a). Urbanization in the southeastern U.S. is increasing at some of the fastest rates in the country as population growth increases in that region. Central Florida, and specifically the Orlando metropolitan region, is typical of recent population growth in the southeastern United States. Greater Orlando's population grew by 70% from 1990 to 2009, very similar to the mean population growth of other major cities in the Southeast (Chapter 2).

Despite rapid urbanization in greater Orlando, numerous freshwater, forested wetlands remain within the urbanized areas (Chapter 2). Freshwater wetlands are categorized as either hydrologically connected or hydrologically isolated and isolated wetlands have less protection under federal U.S. laws (SWANCC v. U.S. Army Corps of Engineers 2001; Craig 2002). Isolated wetlands have a higher risk of being destroyed during urbanization because they are often embedded in an upland matrix that is easily drained. In contrast, hydrologically connected wetlands are often in riverine systems where urbanization is difficult. It is important to note that despite being legally categorized as isolated because of physical isolation, non-navigability, and rare surficial hydrological connections, isolated wetlands are typically coupled to surface water and/or groundwater systems (Whigham and Jordan 2003). Many isolated wetlands in regions with flat topography, like central Florida, have hydrological connections via subsurface hydrology or sheet flow during significant rainfalls. In addition, the cumulative area of isolated wetlands can rival that of hydrologically-connected wetlands, especially in Florida and other portions of the relatively flat Coastal Plain (Semlitsch and Bodie 1998, van der Valk and Pederson 2003). In this paper, I focus on isolated wetlands within a rapidly urbanized landscape because they are relatively vulnerable to destruction and/or degradation (Chapter 2) and rapidly become surrounded by urban land use with potentially subtle (in human terms) but long-lasting consequences for ecosystem services and biodiversity.

Urban wetlands provide valuable ecosystem services (Xu et al. 2009, Haag and Lee 2010) and are an important habitat for native species, including threatened and endangered species (Brandt and Ewel 1989, Ewel 1998, McKinney 2002). Understanding the effects of urbanization on urban wetlands is important to maintaining those services and conserving their biodiversity. Like natural wetlands in the southeastern U.S., many urban wetlands are dominated by the deciduous conifer cypress (*Taxodium distichum*). Two varieties of cypress are recognized, bald cypress and pond cypress, and I was most likely dealing with pond cypress, but I will refer to *T. distichum* in this study simply as cypress. In virgin stands of cypress, adults can average 400-600 years old with some as old as 1,200 years old. While most cypress stands have, at some point, been logged, second-growth stands have been shown to reach heights of 30m (Burns and

Honkala 1990). Isolated wetlands dominated by cypress are called “cypress domes” because trees are taller in the middle and shorter around the edge. These are important habitats for multiple species (Brandt and Ewel 1989, Ewel 1998, McKinney 2002). Cypress domes provide three practical advantages for studying urbanization effects on natural systems: (1) cypress trees are easily distinguished on color infrared photographs (Chapter 1) and thus habitat fragmentation (Chapter 1) and cypress demographic studies across large spatial scales are possible; (2) cypress domes comprise separate cypress populations that enable a naturally-replicated system to test for general patterns across an urbanization gradient; and (3) urbanization of cypress domes occurs rapidly relative to the lifespan of cypress trees, meaning that demographic effects of urbanization can be readily evaluated by quantifying juvenile and adult trees.

Cypress has very specific germination requirements that I hypothesized should be affected by urbanization. Cypress requires saturated but not flooded soils in order to germinate and seedlings must remain above water level for the first year in order to survive (Demaree 1932). Urban stormwater systems often divert incoming rainfall into retention areas to avoid flooding roads and buildings. Cypress domes that remain in urban areas may be used in stormwater systems as retention ponds, or they may be drained to reduce flooding risk. Either scenario alters the naturally variable hydrology of isolated wetlands and likely affects cypress recruitment.

Urbanization also changes the fire regime in which multiple species have evolved. Florida is a naturally pyrogenic landscape, meaning that fire is required to maintain many native ecosystems (Mitchell et al. 2006, Slapcinsky et al. 2010), including cypress domes (Penfound

1952, Marois and Ewel 1983, Casey and Ewel 2006). Fires are suppressed in urban areas in order to prevent burning of homes and other real estate. Fire suppression in cypress domes allows for encroachment of other woody vegetation that may out-compete or shade out cypress seedlings and reduce seed production that is stimulated by fire (Ewel 1995). I hypothesized that the combined effect of urbanization on hydrology and fire regime will reduce recruitment of cypress in isolated cypress wetlands and predicted that recruitment would decrease along an urbanization gradient (i.e., wetlands embedded in natural, agricultural, and urban landscapes).

Methods

Identifying cypress domes

Color infrared aerial photographs and land cover data from 2004 were obtained from the St. Johns River Water Management District for Orange and Seminole counties in the Orlando region of central Florida, USA (28°36’N, 81°18’W, Chapter 2). Using ArcGIS 9.2 (ESRI 2006), polygons identified as forested wetlands in the land cover data were extracted and overlaid on the color infrared aerial photography. At a 1:12,000 scale, the entire study area was scanned and the wetlands observed in the forested wetlands data layer were removed, added or modified to create the cypress dome layer. This manual processing technique was more accurate than automated techniques. Cypress wetlands that were in close proximity to riverine habitats were removed in order to obtain a data layer of “hydrologically isolated” cypress domes.

Determining urbanization gradient

In order to quantify the urbanization intensity of each cypress dome, I categorized land cover surrounding each cypress dome. I first created a buffer in ArcGIS v.9.2 (ESRI 2006) around each cypress dome equal to the average nearest neighbor distance (263 m). Based on descriptions provided with the land cover data layer, five potential land cover categories were identified: natural, agriculture, low urban, medium urban, or high urban. For example, land cover descriptions such as golf courses, recreation, and low density housing were classified as low urban and descriptions such as crops, cattle operations, and citrus groves were classified as agricultural. Principal Component Analysis (PCA) was used to reduce the proportions of each of the 5 land cover categories within the buffer to two multivariate axes. Each axis was then plotted against each of the 5 original land cover proportions. Each graph was evaluated and a range of axis values that represented that category was estimated, based on where the majority of points fell on the graph. For example, when each axis was plotted against the agricultural proportions in each buffer, the majority of points that were high in agriculture were less than -0.5 for axis 1 and between -1 and 1 on axis 2. The ranges obtained from the graphs were used to assign each cypress dome into one of the 5 categories. Canonical Discriminant Analysis was used to test the categories and 92.4% of the cases were classified correctly (Figure 6), which I considered sufficient to represent the urbanization gradient.

Field data collection

Sixteen cypress domes, 8 small (less than 0.5 ha) and 8 large (greater than 0.5 ha) were randomly selected from each urbanization category for sampling. Random points were generated within each cypress dome to establish enough100 m^2 plots (at least two) to cover 2% of the area. Preliminary analysis compared data obtained from random points that covered 1%, 2%, 3%, and 5% of dome area and no significant difference was found among percentages. I sampled plots to equal 2% of the area of the dome in order to obtain sufficient sample size. Preliminary analysis also found that no trees less than 2 m height had cones, but trees > 2m could have cones. I identified any tree < 2 m height as a juvenile, and trees > 2 m height were considered adults. Within each plot, the number of adults and the number of juveniles were recorded.

A vegetation index was also recorded for each plot by taking a picture, at a distance of 10 m, of a 0.9 m x 1.5 m piece of blue vinyl displayed vertically at a height of 2 m in the plot. MVH (Measuring Vegetation Health) Analyzing Digital Images software (Pickle and Kirtley 2004) was used to quantify the area of blue visible through the vegetation. The vegetation index was calculated as 1- (visible blue area / total area of the sign).. Two such vegetation index values were obtained at each plot. Vegetation index values range from 0 to 1 with 1 being the greatest amount of vegetation present.

GIS variables

During field sampling, it became apparent that additional *a posteriori* variables may be necessary to explain the variation in juvenile cypress recruitment. Using ArcGIS (ESRI 9.2 2006), distance from the plot to the wetland edge was calculated as the proportion of the wetland radius. For cypress domes categorized as urban, time since urbanization was calculated from Orange and Seminole County property parcel databases (natural and agricultural cypress domes had no time since urbanization). Cypress dome area was also calculated in GIS and used as a predictor variable in additional analyses.

Differences in recruitment among urbanization categories

Recruitment was analyzed as either the simple number of juveniles or the ratio of juveniles to adults. The number of juveniles was compared among urbanization categories using a zero-inflated Poisson regression model (pscl package; Zeileis et al. 2008) in R (R Development Core Team 2011), with distance to edge of wetland as a covariate. A chi-squared test on the difference of log likelihoods was used to determine if this model was significantly better than the null model (Zeileis and Hothorn 2002). A Vuong test was used to evaluate if the zero-inflated Poisson regression model was significantly better than a simple Poisson model (Vuong 1989). This procedure was repeated with different grouping variables to test for significant differences between (a) non-urban (i.e., natural and agricultural) and urban cypress domes and (b) agricultural cypress domes and all other categories.

The juvenile:adult ratio normalized the number of juveniles to the adult population size, but a substantial number of zeros prevented transformations to meet normality or variance assumptions of traditional ANOVA analyses. Instead, I used Monte Carlo simulation tests (1000 permutations) in R (R Development Core Team 2011) to test for significant differences in juvenile:adult ratio among urbanization categories.

Factors affecting recruitment in urban domes

In order to include distance to the edge of the wetland in analyses, plots were analyzed as independent samples using a mixed effects model to account for variation among domes. Mixed effects models analyze covariates separately as fixed effects or random effects. Random effects are not parameters but are unobserved random variables in which the levels observed represent a random sample from all possible levels (Bates 2010). The variation among domes was accounted for by analyzing the data with dome ID as a random effect. Mixed effects models were analyzed in R v2.13.0 (R Development Core Team 2011) using the lme4 package (Bates et al. 2011).

In order to evaluate the effect of time since urbanization on juvenile recruitment, which is not available for natural and agricultural domes, urban domes were analyzed separately. As above, juvenile:adult ratio was not significantly correlated with response variables due to the large number of zeros in the data, so presence or absence of juveniles was used as the response variable in mixed effects logistic regressions. Predictor variables in models included various combinations of distance to the edge, area of cypress dome, vegetation index, time since urbanization, and PCA Axis 2. PCA Axis 1 distinguished between natural, agricultural, and urban domes while PCA Axis 2 distinguished between the different levels of urbanization (Figure 1). I selected the best model as the one having the lowest Akaike's Information Criteria (AIC; Akaike 1973; Burnham & Anderson 2001) value and highest weight. Model weights indicate the likelihood of each model in comparison to the other models. Thirty total models were compared to determine the best predictors for juvenile:adult ratio in urban cypress domes. Relative variable importance values were also calculated by adding the weights of each model in which a particular variable appeared. Relative variable importance values were calculated using all thirty models.

Factors affecting recruitment in natural and agricultural domes

Juvenile:adult ratio (log transformed) was used as a response variable in linear mixed effects regressions, where predictor variables were distance to the edge of the wetland, area of cypress dome, vegetation index, and PCA Axis 1. P-values are not provided in a linear mixed effects model produced by the lme4 package because it is currently unknown how to calculate the denominator degrees of freedom (Bates et al. 2011). Markov chain Monte Carlo simulations with 10,000 permutations were conducted and p-values were calculated. P-values based on the t statistic with the upper bound for the degrees of freedom were also calculated (Baayen 2011). I selected the best model using AIC as the model with the lowest AIC value and highest weight. Model weights indicate the likelihood of each model in comparison to the other models. Fifteen total models were run to determine the best predictors for juvenile:adult ratio in natural and agricultural cypress domes. Relative variable importance values were calculated using all 15 models.

Projection to other cypress domes in space and time

In order to project recruitment to cypress domes not sampled, I needed to account for random effects in cypress domes. Due to the random effects in mixed effects models, multiple intercepts are generated for every regression equation, yielding one intercept for each cypress dome. The random intercepts for the top urban and top natural/agricultural model (above) were extracted and determined to be normally distributed. Using the mean and standard deviation of the normal curve generated from the intercepts, 100 random numbers were generated for each of the cypress domes for which I were going to project recruitment. In order to account for variation in the distance to the edge, 100 random points were generated within each cypress dome and the distance to the edge was calculated for each. Using the randomly generated intercepts and distance to the edge values, along with the other fixed effects values, 100 predicted regression values for each dome were calculated. The 100 predicted values were then averaged to obtain 1 value of either probability of juvenile presence (for urban cypress domes) or juvenile to adult ratio (natural and agricultural cypress domes). The regression predicted values were used to create maps in ArcGIS version 9.3 (ESRI 2009).

Results

Differences in recruitment among urbanization categories

Urbanization category, with distance to the edge as a covariate, was a significant predictor of the number of juveniles using the zero-inflated Poisson regression model ($p = 0.02$), which was significant compared to the null model (chi-squared = 30.85, df = 4, $p<.0001$) and a significant improvement over a standard Poisson model (Vuong test; $p<0.0001$). Urbanization groups no longer significantly predicted the number of juveniles if natural and agricultural domes were grouped together and compared to urban domes grouped together ($p = 0.0994$). However, grouping agricultural domes as separate from all other categories combined yielded a significant prediction of the number of juveniles ($p < 0.0001$), showing that agricultural cypress domes had a significantly different number of juveniles than all other categories. Monte Carlo simulations also showed significantly different juvenile to adult ratio among the urbanization categories ($p < 0.0001$). Overall, cypress did not follow a simple urbanization gradient (from natural to agricultural and low-, medium-, and high-urban). Instead, agricultural cypress domes (which were primarily in cattle ranches) had higher recruitment than other categories (Figure 7).

Factors affecting recruitment in urban cypress domes

In urban cypress domes, time since urbanization ($z = -2.22$, $p = 0.026$) and distance to the edge of the wetland ($z = -2.51$, $p = 0.01$) best explained the juvenile:adult ratio (Table 3; Figure 8). Using a presence/absence threshold of 0.5 (as in a binomial coin toss), this model based on time since urbanization and distance to the wetland edge (Table 3) correctly predicted 94% of absences and 93% of presences. Less cypress recruitment occurred in the centers of cypress domes than on the edges, and recruitment drops precipitously at about 20 years after urbanization (Figure 8). Consistent with that model, 9 out of the 48 sampled cypress domes had time since urbanization values ranging from 22 to 60 years and recruitment was not seen in any of them. In decreasing order, the relative variable importance values were: time since urbanization (0.988), distance to the edge of the wetland (0.893), Axis 2 (0.287), vegetation index (0.037), and area of cypress dome (0.028).

Factors affecting recruitment in natural and agricultural cypress domes

In natural and agricultural cypress domes, the model with PCA Axis 1 ($P_{MCMC} = 0.066$, $t = -1.92$, $P_t = 0.080$), distance to the edge of the wetland ($P_{MCMC} = 0.030$, $t = -2.71$, $P_t = 0.005$), and area of the cypress dome ($P_{MCMC} = 0.0001$, $t = 3.691$, $P_t = 0.000$) was the best model (Table 4; $R^2 = 0.764$). Juvenile:ratio was negatively correlated with PCA Axis 1 and distance to the edge of the wetland and positively correlated with cypress dome area (Figure 9; lower Axis 1 values correspond to agricultural domes – see Figure 6). This result indicates that the greatest cypress recruitment is occurring on the edge of large, agricultural cypress domes, rather than cypress domes in natural lands. In decreasing order, the relative variable importance values were:

area of cypress dome (0.986), distance to the edge of the wetland (0.881), PCA Axis 1 (0.656), and vegetation index (0.267).

Projection to other cypress domes in space and time

Using the mixed effects regression models allowed us to estimate the probability of juvenile presence in urban cypress domes and a juvenile:adult ratio for natural and agricultural cypress domes throughout the two-county study area. Using a presence/absence threshold of 0.5, only 114 of 728 urban cypress domes (15.7%) are estimated to be recruiting cypress and those cypress domes typically fall on the periphery of urbanization (Figure 10). In addition, juvenile:adult ratios in natural and agricultural cypress domes show high recruiting and low recruiting cypress domes spatially intermixed, with the highest recruitment projected to occur in the largest cypress domes (Figure 11).

Destruction and degradation caused the loss of 20.2% and the conversion of 25.8% of the natural cypress domes to urban categories from 1984 to 2004 (Chapter 1). During the same time period, 25.6% of the agricultural cypress domes were lost and 3.1% were converted to urban categories. Assuming that recent urbanization patterns continue at the same rate, I projected that ~89% of the cypress populations in cypress domes that are currently recruiting will fail to recruit in 100 years, and that most (87%) remaining cypress populations that still recruit will be on agricultural lands (Table 5).

Discussion

Surprisingly, I found that natural and urban cypress domes have lower cypress recruitment but agricultural cypress domes generally maintain higher levels of recruitment. Thus cypress recruitment did not follow a natural-to-urban gradient as expected, and this result is important to the conservation and management of isolated wetlands dominated by cypress throughout its range. The main factors driving cypress recruitment were time since urbanization (among urban land use classes), distance to the wetland edge, and wetland area.

Alterations to both hydrology and fire regimes should reduce recruitment in cypress domes. Both alterations affect cypress recruitment in urbanized areas but an altered fire regime likely occurs in natural areas as well. In natural fire regimes, fire often burns wetlands until it reaches enough moisture to run out of fuel (Frost et al. 1986). Many managers of natural (typically forested) lands prevent prescribed or wild fires from burning through wetlands (Frost et al. 1986) in order to prevent muck or peat fires, and I observed several natural cypress domes with fire breaks to prevent prescribed fires from encroaching into the wetland. Muck or peat fires arise from overdrying of organic wetland soils and can lead to underground smoldering than can last several weeks (Reardon et al. 2007, Leeds et al. 2009) and cause persistent smoke plumes and reignited wildfires – a severe problem to be avoided near a metropolitan region. Our results suggest that fire management practices on natural lands may lead to lower cypress recruitment in cypress domes, equivalent to that seen in urbanized domes. Based on this result, I recommend that managers of natural lands evaluate cypress domes on their lands for the actual presence of muck or peat; cypress domes with relatively short hydroperiods (i.e, substantial periods of oxidative soil conditions) are unlikely to accrue substantial organic matter and should not cause muck or peat fires. In addition, a natural fire regime will prevent build up of organic materials that would lead to muck fires (Penfound 1952, Casey and Ewel 2006). Natural wetlands can be subjected to prescribed fires and in turn help restore and maintain cypress recruitment.

Fire breaks were not present in the agricultural cypress domes I sampled, most of which occurred on cattle ranches. Prescribed fires are common in cattle ranches to suppress woody vegetation in pastures and stimulate forage grasses growth. Due to the lack of fire breaks, I expect that fires on ranches are often allowed to burn into cypress domes. Interestingly, this practice may more closely mimic natural fire regime than fire management practices in natural forested lands and has maintained recruitment in agricultural cypress domes because more frequent fire leads to decreased competition and more available sunlight for cypress seedlings. Ranchlands also have numerous cattle that can contribute to increased cypress recruitment. Cattle forage on multiple types of vegetation and can clear the understory, limiting competition for cypress seedlings. Nutrient input from cattle may also increase cypress recruitment. The combined effect of increased fire and cattle presence could help explain the higher recruitment in agricultural cypress domes.

Urban cypress domes have virtually no fire regime and tend to have altered hydrology (either longer to permanent hydroperiod or drained) relative to the variable hydrology of non-urban isolated wetlands. Changes to fire regime and hydrology appear to be consistent across the three levels of urbanization (low, medium, or high) because levels were far less important to cypress recruitment than was time since urbanization. Recruitment dropped substantially around

20 years post-urbanization and we sampled cypress domes with varying ages including several from 20 to 60 years post-urbanization, none of which showed recruitment. With good seed crops every 3-5 years in cypress (U.S. Department of Agriculture 1974), I would expect multiple cohorts of juveniles to have recruited in cypress domes 20 to 60 years post urbanization. While it is unknown how long it takes for a tree to reach 2 m (and thus be classified as an adult in this study) and that time period is likely to vary dependent on nutrient availability, I would estimate it may take 10 years or less. Thus, if recruitment was occurring in cypress domes 20 post-urbanization, juveniles would have been present.

Prior to ~20 years, the most important variable in determining presence or absence of juveniles is distance to the edge of the wetland (Figure 8). This result is consistent with the fact that many urban cypress domes are used for stormwater retention, which serves to hold more water longer in the center and thus have conditions favorable for germination only on the edge of the wetland. These cypress domes will continue to recruit at the edge of the wetlands until around 20 years post-urbanization when the encroachment of other vegetation (including nonnative, invasive species) becomes evident enough to completely halt recruitment.

Wetland area and distance to the wetland edge were the most important variables to predict juvenile:adult ratio in natural and agricultural cypress domes. Larger cypress domes have more edge and often have longer hydroperiods allowing for standing water in the center and increased saturation of the soil near wetland edges. Saturated, but not flooded soils are ideal for cypress germination and seedling survival (Brandt and Ewel 1989, Burns and Honkala 1990). Potentially better hydrology and reduced competition at the edge as a result of frequent prescribed fire (provided there are no fire breaks) likely contribute to the effect of wetland size on cypress recruitment in natural and agricultural cypress domes.

Overall, management in the form of both prescribed fire and altered hydrology in urbanized areas will lead to the loss and degradation of hundreds of cypress populations within the Orlando metropolitan area (Chapter 1). The same processes will also halt recruitment in remaining urban populations and the existence of those populations will be tied to the lifespan of the current adults. Urbanization is essentially permanent, and will not be practically altered to preserve cypress populations rather than prevent flooding of buildings and widlfires. However, reduced urban sprawl would mitigate the ongoing extirpation of viable cypress populations that is happening in the area.

Management practices in natural lands are far more amenable to change, and a small change in prescribed fire practice (i.e., burning through cypress domes with seasonal or ephemeral hydroperiods) should permit ongoing cypress recruitment and not lead to muck or peat fires. In addition, preliminary surveys (soil cores, pits, visual records of surface water) can readily ascertain which wetlands in natural areas can be burned (as often happens in cattle ranches) and which wetlands will need fire breaks. This simple change in practice should have a strong effect on recruitment and long-term viability of the dominant species in many wetlands of the southeastern U.S. within natural lands. In the absence of this simple change in management practice, thousands of wetlands may remain on regional natural lands, but cypress will fail to recruit within decades in many wetlands, and the once typical and valued “cypress domes” will be replaced by a mixture of other vegetation, with unknown consequences for regional ecosystem services and biodiversity. Moreover, cypress will be relegated to riparian zones and largely obliterated from the many isolated wetlands in urban areas throughout the region, with potential genetic and demographic effects.

CHAPTER 4: POPULATION GENETIC STRUCTURE OF CYPRESS (*TAXODIUM DISCTICHUM*) IN ISOLATED WETLANDS IN AN URBAN LANDSCAPE

Introduction

Urbanization has caused loss and degradation of cypress domes in Orlando (Chapter 2). Alterations to hydrology and fire regimes have also caused lower recruitment in urban cypress domes (Chapter 3). I hypothesized that the same alterations to hydrology in urban areas would limit dispersal and gene flow in urban areas. Cypress cones float and in natural areas cypress are likely dispersed through ground water and through surficial connections during significant rainfalls (Middleton 2000). Urbanization alters the hydrology and removes natural water connections leading to a reduction of gene flow among urban wetlands. Limited gene flow among wetlands would likely lead to higher inbreeding as the juveniles in the population could only recruit from adults within a population. Since adults were recruited pre-urbanization and juveniles post-urbanization, I expected to see a genetic differentiation between the two groups. I hypothesized that urban cypress domes would have lower gene flow among wetlands and juveniles in urban wetlands would have higher levels of inbreeding than their adult counterparts.

Methods

I attempted to analyze microsatellite markers for *Taxodium distichum* in order to test this hypothesis. Microsatellite markers are short tandem repeats and are highly variable markers often used in population genetic studies (Jarne and Lagoda 1996). Genetic samples were collected from 21 randomly selected populations from across all 5 urbanization categories. Within each cypress domes, 30 points were randomly generated using ArcGIS v. 9.2 (ESRI

2006). At each point the nearest adult and nearest juvenile (if any were present) were located and needles were collected from each. In some instances, adult trees were so tall that the lowest branch with available needles was out of reach. In those cases, a slingshot was used to shoot a fishing weight attached to fishing line into the tree and over an available branch. I attempted to get the fishing weight to drop back down the other side of the branch and was then able to break the branch or shake it in order to obtain needles. Once collected, needles were dried and stored in Dri-Rite desiccant until DNA extraction could be completed.

Microsatellite primers for this species did not exist and had to be developed for this study. I successfully created a microsatellite library based on a CA repeat because dinucleotide repeats are common in plants (Jarne and Lagoda 1996). I obtained ~50 sequences throughout the genome that were positive for repeat regions. From those, I created primer pairs from the flanking regions of those repeats using Primer 3 (Rozen and Skaletsky 2000). I ordered 25 of the primer pairs and attempted to amplify those repeat regions. I was initially not able to get a successful PCR using the primer pairs. After several attempts using a variety of different PCR conditions, I was able to get between 8-10 primer pairs to amplify. The conditions required 2 times the amount of MgCl initially tested and annealing temperatures around 44-46° C. While annealing temperatures can vary by locus and species, I had not found literature with annealing temperatures that low; annealing temperatures are generally between 50-65° C (Tsumura et al. 1997, Soranzo et al. 1999, Hoffman et al. 2003).

After verifying that amplification was possible, I extracted DNA from ~875 samples of cypress needles using both a modified CTAB protocol and Qiagen DNeasy Plant Mini Kits. I amplified several individuals at approximately 10 loci in order to verify that proper microsatellite allele peaks could be visualized in a fragment analysis. I analyzed samples using both a Beckman Coulter CEQ 8800 and an Applied Biosystems, Inc ABI 3730 DNA Analyzer. I obtained electropherograms for all loci analyzed. Some primer pairs were removed from future analyses because they either did not show amplification or the amplified loci were monomorphic. At that point, there were 6 polymorphic loci included in future analyses. Three of those loci appeared to be polyploid, with one individual typically amplifying more than two alleles and up to 6 alleles (Figure 12).

Polyploidy is common in angiosperms, but only one family of gymnosperms is known to contain polyploids, Cupressaceae. This is the same family as *Taxodium distichum* which is known to be a diploid organism (Ahuja and Neale 2002, Kado et al. 2006). Conifers have a large genome size, ranging from ~6,500 Mb to ~37,00 Mb and Ahuja & Neale (2005) suggested that ancient polyploidy or gene duplication could be responsible. If ancient polyploidy or large segments of the genome had been duplicated for *Taxodium distichum* in the past, this may explain the multiple alleles seen in this study. With this explanation in mind, all of the samples were amplified at 6 loci, sent to the University of Arizona Genetics Core and analyzed using an ABI 3730 DNA analyzer. Electropherograms were evaluated using STRand software (Toonen and Hughes 2001).

Preliminarily, 8 of the 21 populations (Figure 13) were scored and genotypes were recorded. The allele sizes in about half of the loci amplified did not match the expected sizes obtained from the Primer 3 output and it was often difficult to distinguish the genotypes from “noise” in the electropherograms. There were also “alleles” present in the negative controls that scored similar to other individuals. There was a great deal of similarity between samples with most individuals having the same alleles at each locus and I was unsure if the data showed real alleles or non-specific amplification because the annealing temperatures were so low. In order to find this out and evaluate the population structure using the current data, I ran several analyses on the preliminary subset of populations.

Following methods in Andreakis et al. (2009) for analyzing polyploidy data, I converted all genotype data to a binary matrix where each allele or amplification variant (AV) was given a 0 or 1 for presence or absence, respectively in that individual. Data were then analyzed as dominant markers where each possible AV was considered independently instead of codominantly as is usual with microsatellites. AV’s were combined into one banding pattern for each individual and the resulting pairwise binary matrix was used to analyze differences between populations. A regular analysis of molecular variance (AMOVA) was performed in GenAlEx v. 6.41 (Peakall and Smouse 2006) and pairwise Φpt estimates were calculated to obtain gene flow levels between populations and the number of immigrants (Nm) = 0.25(1 – Φpt)/Φpt. Pairwise Φpt estimates were calculated and used in a Principal Component Analysis (PCA) to show population differentiation and to conduct a Mantel test to look for isolation by distance.

A Bayesian AMOVA was conducted in Hickory v. 1.1 (Holsinger and Lewis 2003) to estimate population differentiation. Two estimates of population differentiation were estimated, $\theta^{(I)}$ and $\theta^{(II)}$. $\theta^{(I)}$, is most closely related to Wright’s F_{ST} and measures allele frequency variance within a population and assumes a stationary evolutionary process. $\theta^{(II)}$, is most closely related to

Nei's G_{ST} and is a scaled allelic frequency variation measured across contemporaneous populations. It treats populations as a random subsample from all possible populations. Due to the recent loss of several populations of cypress domes (Chapter 2), $\theta^{(II)}$ may be the most accurate estimate of population differentiation. According to the software manual (Holsinger and Lewis 2003), Hickory can infer estimates of f (the within-population inbreeding coefficient) from dominant markers, though these calculations may be unreliable. It is suggested that several models be run including the full model, the f =0 model, and the f -free and $\theta^{(I)} = 0$ null-models (Holsinger and Lewis 2003, Andreakis et al. 2009).

Results

The regular AMOVA shows that 87% of the variation was from within populations and only 13% of the variation was from among populations (Table 6). Pairwise genetic distances were low and did not show an obvious correlation with genetic distances (Table 7). Mantel test confirmed that there was little evidence of isolation by distance (Figure 14). PCA analyses showed that the most obvious factor separating populations were the plate on which they were run (Figure 15). PCR and fragment analyses were done on 96-well plates that would typically hold 2-3 populations per plate. The 8 populations run in the preliminary analyses were run on 3 plates. The DIC values for the Bayesian AMOVA show that the full model is the best model to represent population differentiation. $\theta^{(II)}$ values, the most accurate to represent differences between contemporaneous populations, show extremely low population differentiation at 0.003 in the full model. This shows there is very little structure to the populations analyzed despite the wide variety of distances between populations (Figure 13).

Discussion

Results suggest that the alleles analyzed may not actually be microsatellite alleles. The lack of population differentiation, the presence of "alleles" in negative controls, and the "noise" seen in a majority of the samples all suggest that low annealing temperatures are contributing to non-specific amplification not representative of actual markers. I believe that while I definitively found positive microsatellites in the sequences generated from the microsatellite library development, the primers developed from those failed to amplify actual microsatellite markers. This was verified by the allele sizes not matching the allele sizes from the original sequences input into Primer 3. I had an extremely hard time getting PCR to be successful and was only able to have "success" using one specific brand of taq polymerase, high amounts of MgCl, and annealing temperatures well below most published temperatures. I believe these conditions led to bands on electrophoresis gels that seemed as if they were microsatellite markers. However, when fragment analysis was done and populations were analyzed, they failed to represent what expected microsatellite markers should. The only way to know for sure if the amplified products are actually microsatellite markers and *Taxodium distichum* actually has polyploidy portions of the genome is to clone and sequence several of them to see if the repeats are present in the sequence. Without this information, I can only assume that the genetics analyses in the project failed and I still do not know the effects of urbanization on the population genetics of cypress.

CHAPTER 5: DISCUSSION

Modern human population growth is biased to urban areas, causing increased urbanization of landscapes worldwide, including large population increases in the southeastern United States. The Orlando metropolitan area is typical of the population growth in the Southeast and also has numerous cypress domes, many of which still remain among current urbanization. Urbanization both fragments and disturbs natural ecosystems and causes decreases in native species diversity. The purpose of this study was to evaluate the effects of urbanization on cypress domes in central Florida. Specifically, I tested how urbanization (fragmentation, altered hydrology, and altered fire regime) affected (a) the numbers and spatial pattern of cypress domes in central Florida and (b) the recruitment of pond cypress within cypress domes. I attempted to test (c) gene flow of pond cypress among cypress domes. I then combined information from a & b into a Geographic Information System (GIS) model that depicts historical changes and can be used to predict future effects.

Analyses of historical loss found over 3,000 cypress domes identified in images from1984, of which 26% were lost or degraded (i.e., no longer cypress-dominated) by 2004. Due to changed land use, many remaining cypress domes, formerly surrounded by natural lands, became surrounded by urban lands. These recently urbanized cypress domes were also more spatially clustered. Cypress dome sizes became more homogeneous with the loss and degradation of small cypress domes in natural and agricultural lands and large cypress domes in urban lands. Despite legal protection of these habitats, urbanization, and its accompanying alterations to fire and hydrology regimes, fragmented and degraded wetlands. Urbanization will likely continue to decrease heterogeneity among cypress domes and landscape-level biodiversity of cypress domes range wide will be decreased.

Recruitment analyses indicate that urban cypress domes as well as natural cypress domes had lower recruitment than cypress domes in agricultural areas, mainly cattle ranches. Many land managers place fire breaks around cypress domes in natural areas to avoid burning wetlands and creating long-lasting muck fires that can smolder for several weeks. This practice seems to be limiting recruitment as cypress domes in agricultural areas did not have fire breaks and these cypress domes had higher recruitment. Our results also showed that time since urbanization and distance to the edge were the best predictors of juvenile:adult ratio in urban cypress domes. Recruitment dropped substantially at 20 years post urbanization; previous to that, recruitment occurred near the edge of wetlands where hydrological conditions were most favorable. In natural and agricultural cypress domes, recruitment again occurred near the edge of the wetlands and was higher in larger domes.

While chapter 1 showed significant degradation over a 20 year period and chapter 2 showed substantial reduction in recruitment at 20 years post-urbanization, I believe this may simply be coincidence. I didn't sample cypress domes that degraded from 1984 to 2004 because they were no longer identified as cypress domes in 2004 so I don't know if cypress may have still been recruiting. Also, I only evaluated degradation at a 20-year time interval and it is unknown to what extent degradation may have been occurring at shorter intervals. While it is possible that degradation may reduce recruitment, I did not specifically test this and the 20-year time period observed in both chapters likely has no significance.

If past urbanization patterns continue, ~89% of the cypress domes in the study area now recruiting could cease recruitment by 2104. I suggest that reducing urban sprawl and enacting prescribed burning of natural cypress domes may mitigate this effect but in the absence of management practice changes, cypress recruitment will cease in many isolated wetlands, leading to unknown genetic and demographic consequences. This study illustrates how susceptible cypress wetlands are to urbanization. Without proper management, cypress domes are likely to continue to be lost to urbanization and recruitment may cease in most remaining wetlands. Cypress will then be relegated to riparian zones in urban areas and cypress in isolated cypress wetlands may be at risk.

APPENDIX A: CHAPTER 2 FIGURES AND TABLES

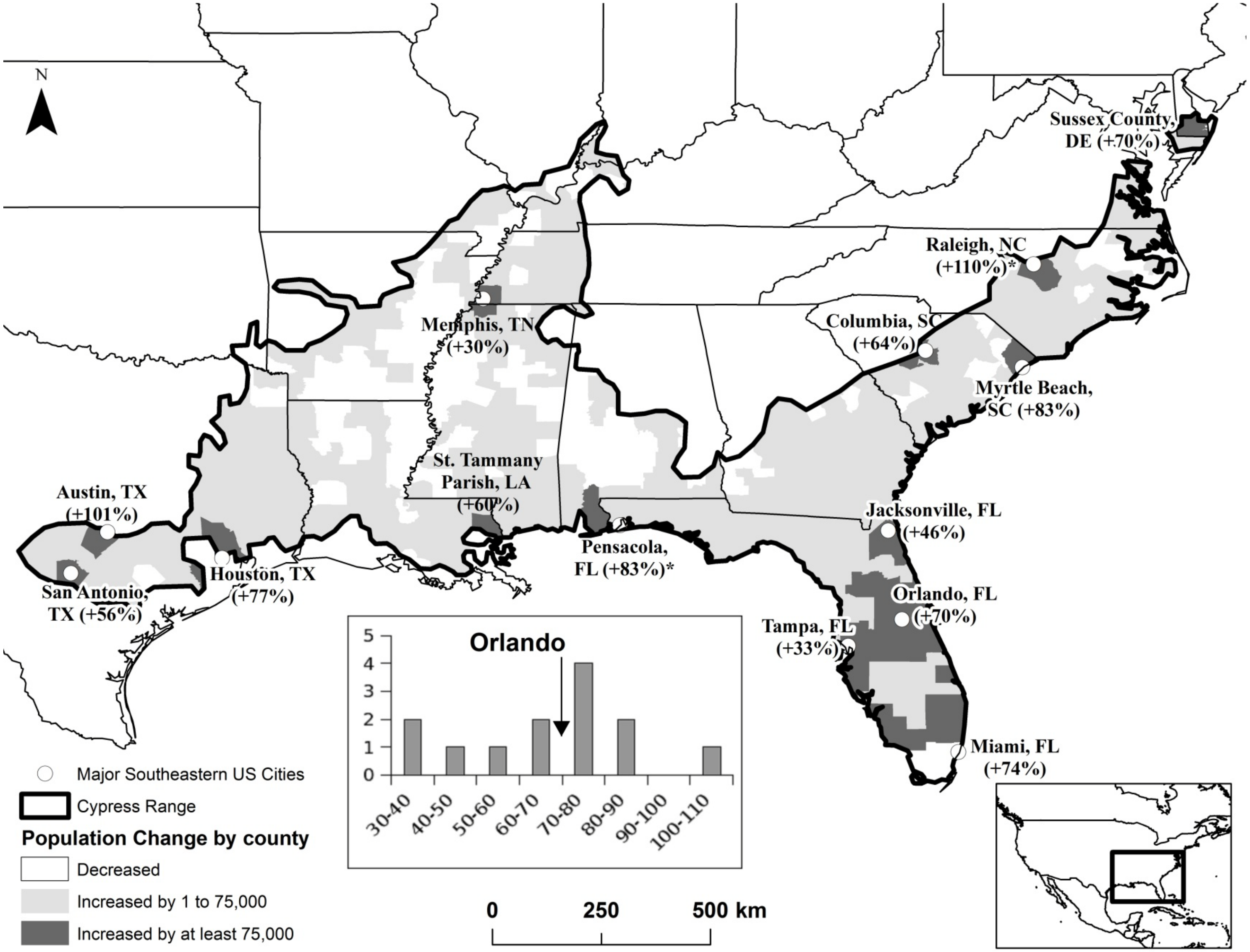

Figure 1. Population change in the southeast U.S. from 1990-2009 and species range of cypress. Cities shown are those where the city (or surrounding counties) had population growth greater than 75,000 people. Counties that grew >75,000 people but lacked a major city nearby are also indicated. Embedded graph is histogram of city/county population growth.

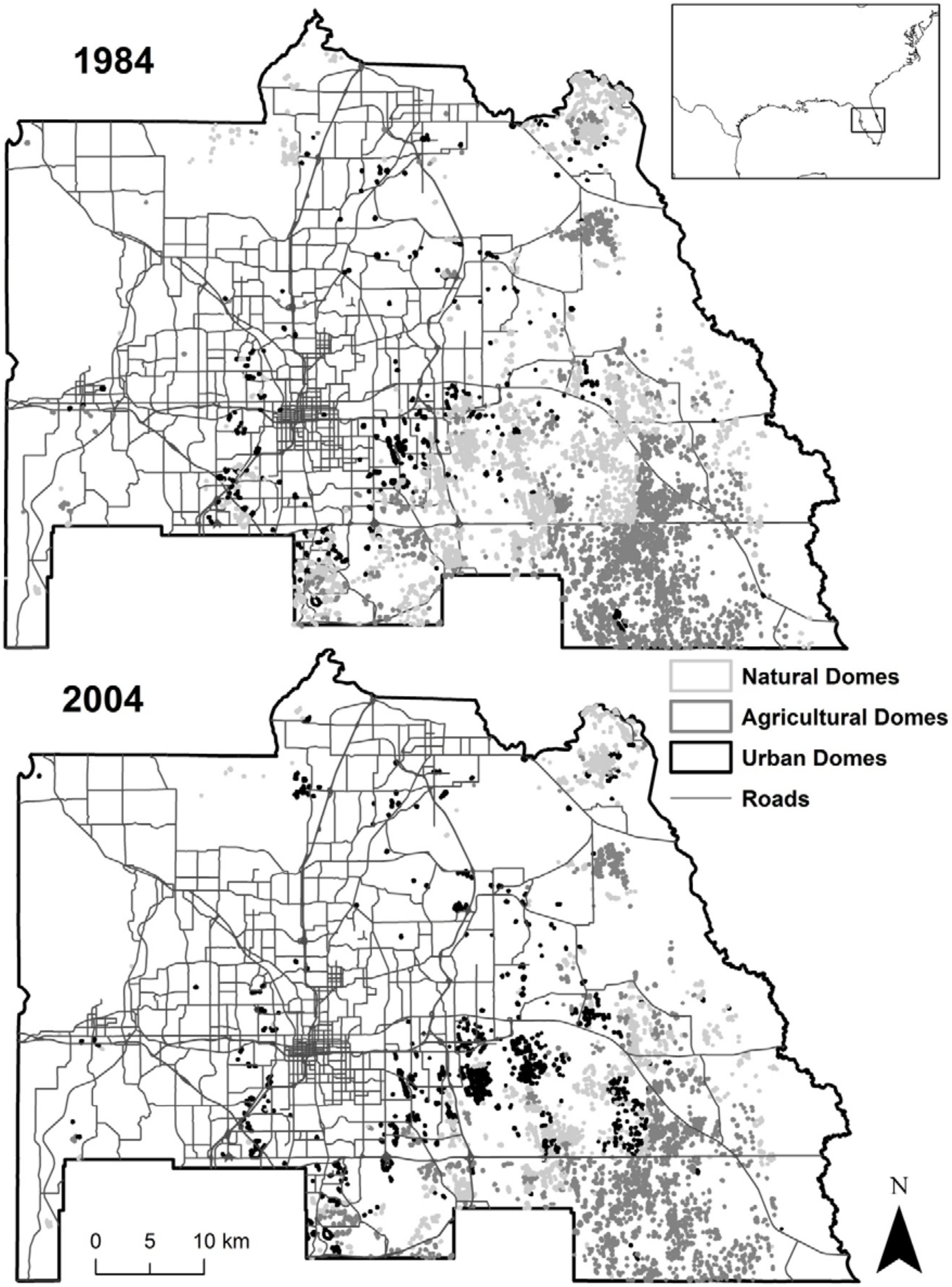

Figure 2. Cypress domes present in the Orlando metropolitan area in 1984 and 2004. Low-, medium-, and high-urban dome categories have been combined and displayed as “Urban Domes”.

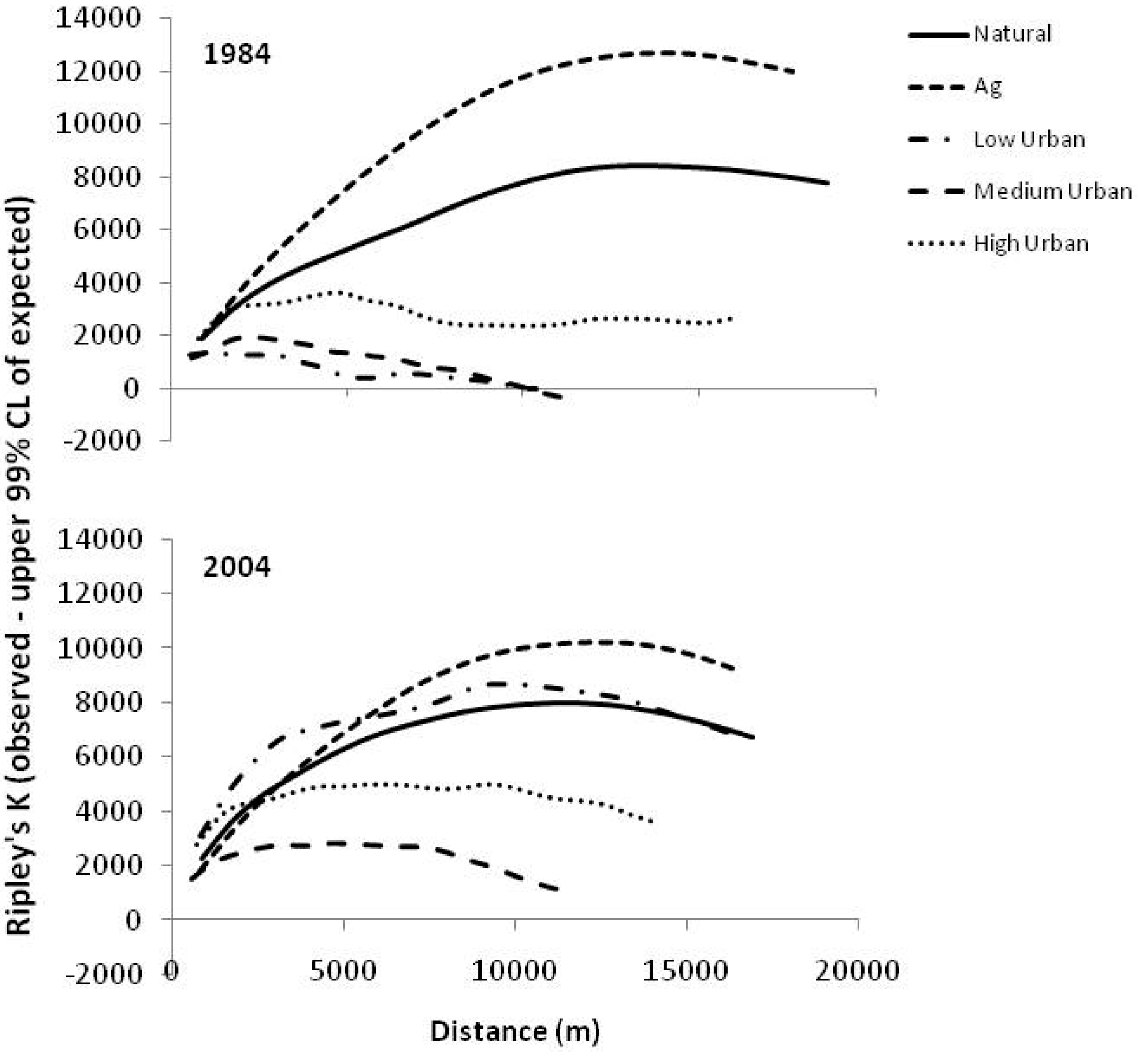

Figure 3. Ripley's K values for 1984 and 2004 cypress domes. Values in the above plots represent [observed values – (upper 99% confidence limit of expected values)]. Thus, values greater than 0 on above plots indicate significant clustering. This shows that low and medium urban cypress domes had less clustering and were close to randomly distributed at 10,000 m in 1984 but by 2004 both categories became more clustered. Natural and agricultural domes became less clustered from 1984 to 2004.

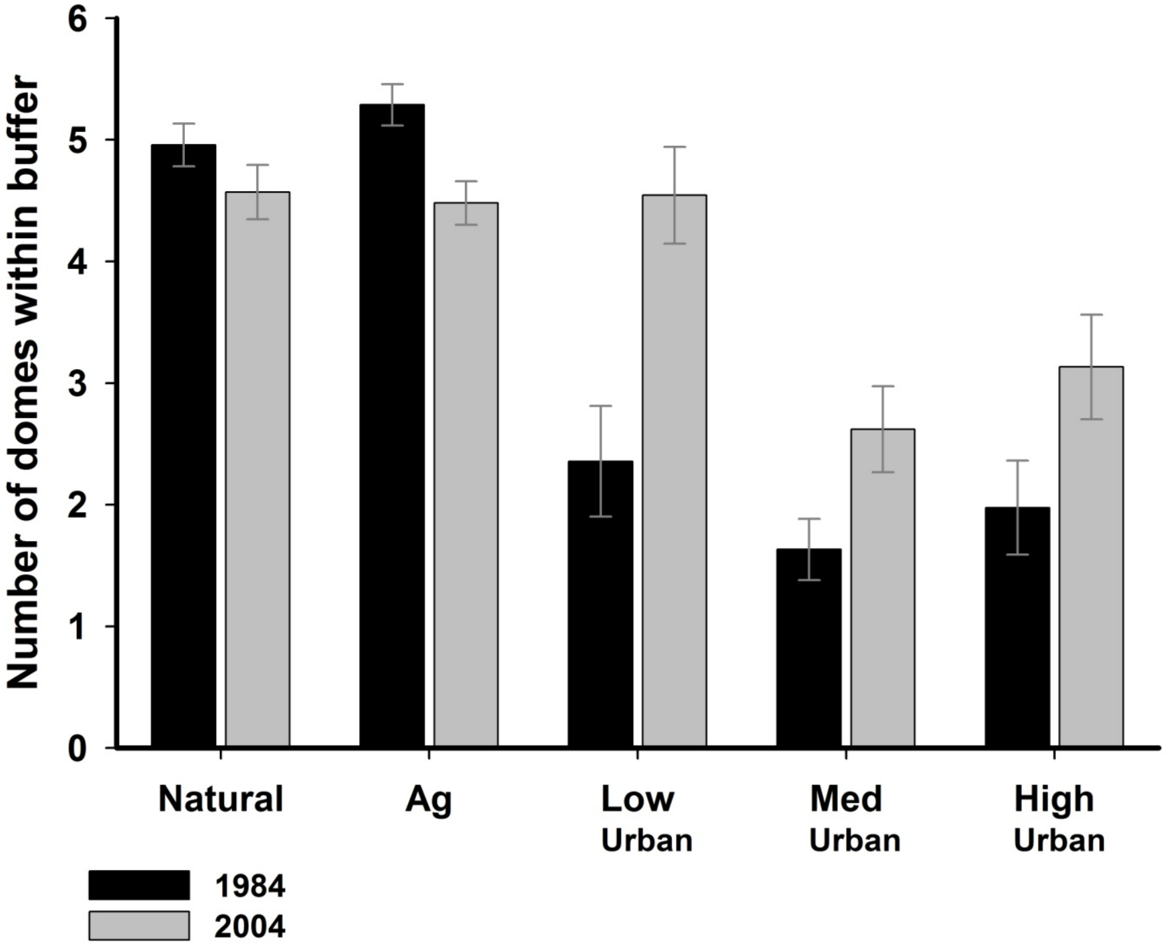

Figure 4. Spatial Isolation Index of cypress domes. Domes were enumerated within a 490 m buffer (twice the nearest neighbor distance for domes present in 1984). Black bars (from 1984) show that natural and agricultural categories grouped together and the urban categories grouped together while grey bars (from 2004) show that the low urban category groups with natural and agricultural categories. This also shows that natural and agricultural cypress domes became less clustered and urban cypress domes became more clustered from 1984 to 2004. Error bars represent 95% confidence intervals.

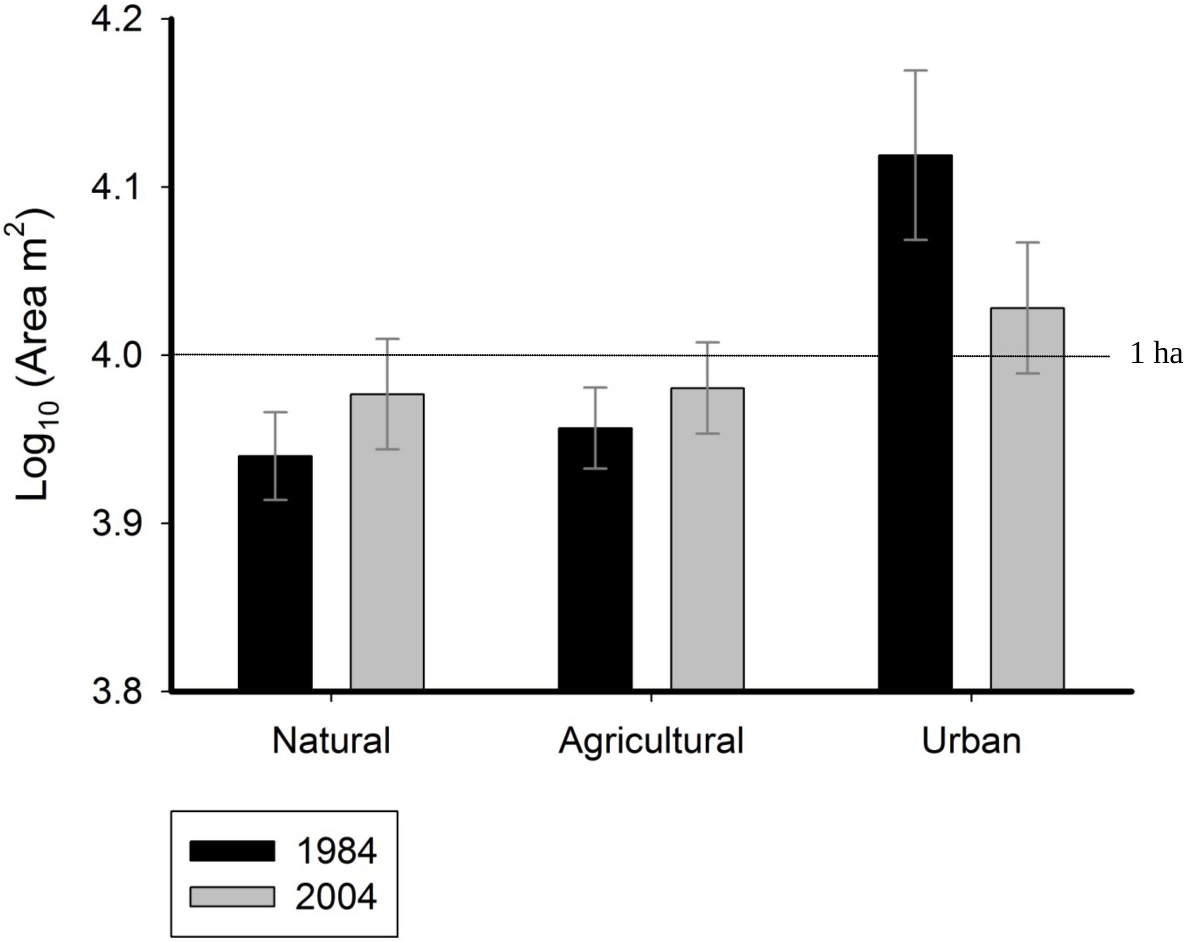

Figure 5. Mean area for cypress domes. Black bars (1984) show a larger difference between natural/agricultural domes and urban domes while the grey bars show all categories are closer to 1 ha. This also shows that the average size of natural and agricultural cypress domes got larger from 1984 to 2004 and the average size of urban cypress domes got smaller during the same time period. Low-, medium-, and high-urban domes have been combined into one “Urban” category. Error bars represent 95% confidence intervals.

Table 1. Number and percent change of cypress domes for each year.

		1984	**% of 84 domes**	**2004**	**% of 2004 domes**	**change**	**% change**
Natural	Number	1517	45%	767	31%	-750	-49%
	Area	2925.9	46%	1379	29%	-1546.9	-53%
Ag	Number	1588	47%	1110	44%	-478	-30%
	Area	2782.9	44%	1927.6	41%	-855.3	-31%
Low Urban	Number	98	3%	294	12%	196	200%
	Area	167.2	3%	602	13%	434.8	260%
Med Urban	Number	109	3%	169	7%	60	55%
	Area	290.2	5%	421.9	9%	131.7	45%
High Urban	Number	81	2%	158	6%	77	95%
	Area	197.2	3%	346.8	7%	149.6	76%
Total	**Number**	**3393**		**2498**		**-895**	**-26%**
	Area	**6363.4**		**4677.3**		**-1686.1**	**-26%**

Table 2. Matrix of urbanization category changes, loss and degradation of cypress domes (number and area) from 1984 to 2004.[a]

		Natural in 2004	Ag in 2004	Low urban in 2004	Med urban in 2004	High urban in 2004	Disappeared	Degraded
Natural	Number	**629 (41.5%)**	130 (8.6%)	220 (14.5%)	79 (5.2%)	92 (6.1%)	122 (8.0%)	245 (16.2%)
in 1984	Area (m^2)	**1326.6 (45.3%)**	244.1 (8.3%)	420 (14.4%)	196.9 (6.7%)	294.5 (10.1%)	129.9 (4.4%)	313.8 (10.7%)
Ag	Number	140 (8.8%)	**992 (62.5%)**	24 (1.5%)	20 (1.3%)	5 (0.3%)	37 (2.3%)	370 (23.3%)
in 1984	Area (m^2)	230.4 (8%)	**1877.9 (67.5%)**	37.9 (1.4%)	38 (1.4%)	8.7 (0.3%)	47.4 (1.7%)	542.5 (19.5%)
Low urban	Number	0	0	**49 (49.5%)**	11 (11.1%)	12 (12.1%)	6 (6.1%)	21 (21.1%)
in 1984	Area (m^2)	0	0	**72.8 (43.5%)**	34.4 (20.6%)	16.9 (10.1%)	10.2 (6.1%)	32.9 (19.7%)
Med urban	Number	0	0	0	**55 (50.5%)**	14 (12.8%)	10 (9.2%)	30 (27.5%)
in 1984	Area (m^2)	0	0	0	**181.2 (62.4%)**	18.3 (6.3%)	29.3 (10.1%)	61.4 (21.2%)
High urban	Number	0	0	0	0	**35 (43.2%)**	11 (13.6)	35 (43.2%)
in 1984	Area (m^2)	0	0	0	0	**87.1 (44.2%)**	27 (13.7%)	83 (42.1%)
Total	Number						186 (5.5%)	701 (20.7%)
	Area (m^2)						243.8(3.83%)	1033.6 (16.24%)

[a] Any differences in numbers from Table 1 are a result of merging of multiple domes into one and splitting of one dome into multiple domes from 1984 to 2004.

APPENDIX B: CHAPTER 3 FIGURES AND TABLES

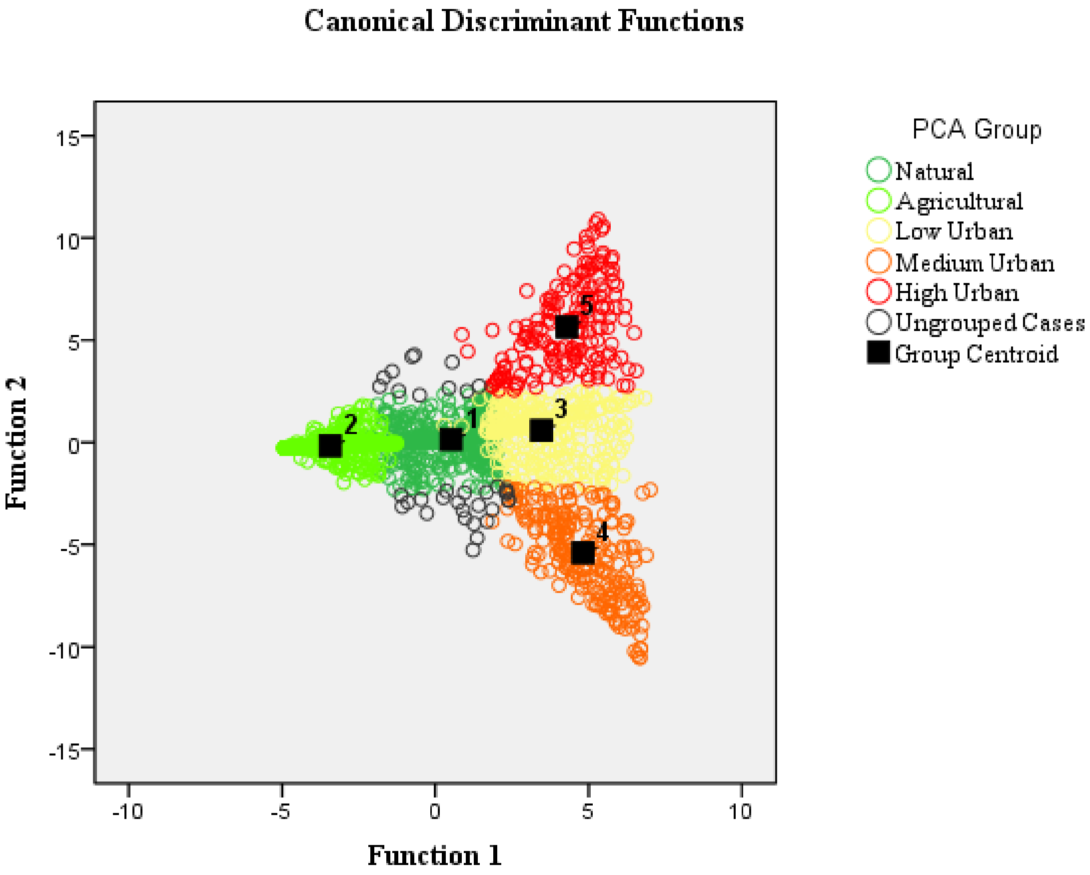

Figure 6. Canonical discriminant analysis results. Functions 1 and 2 correspond to PCA Axis 1 and 2, respectively. Ungrouped cases represent the 7.6% of the cypress domes in which the PCA and Canonical discriminant analysis did not agree. Function 1 (PCA Axis 1) separates natural, agricultural, and urban domes while function 2 (PCA Axis 2) separates low-, medium-, and high-urban cypress domes.

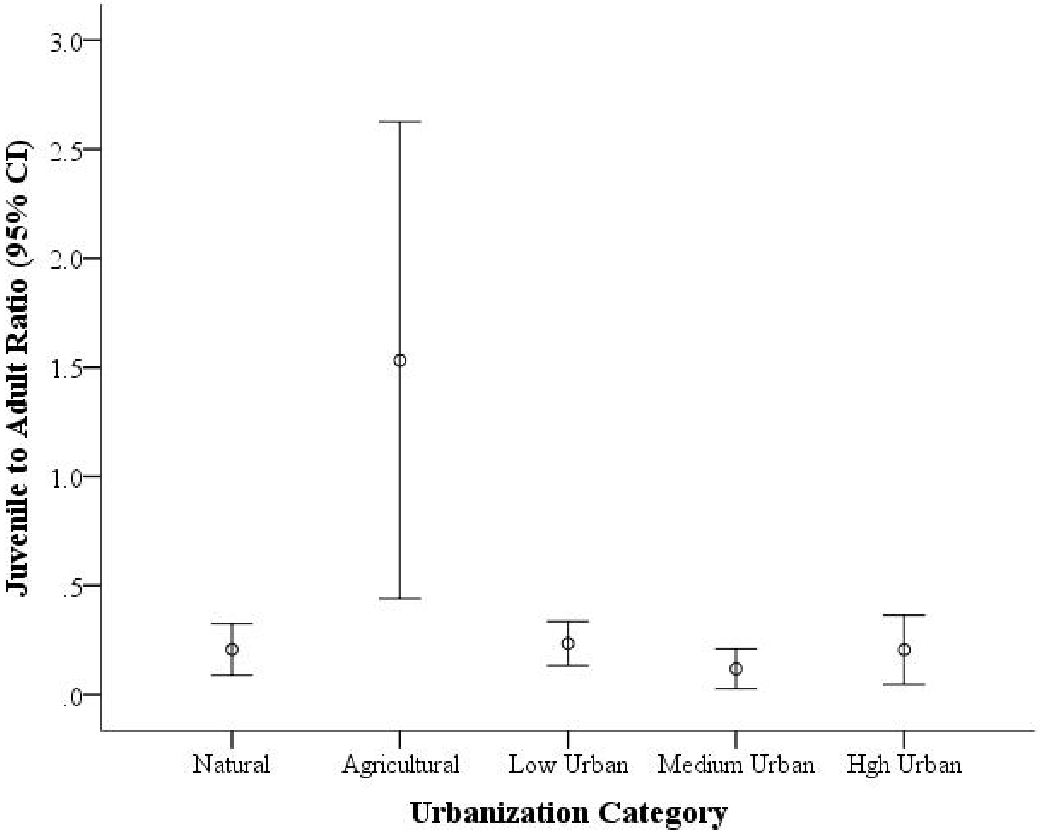

Figure 7. Juvenile:adult ratio among the 5 urbanization categories. Agricultural cypress domes had a significantly higher juvenile:adult ratio than other urbanization categories. Natural and urban cypress domes do not have significantly different juvenile:adult ratio.

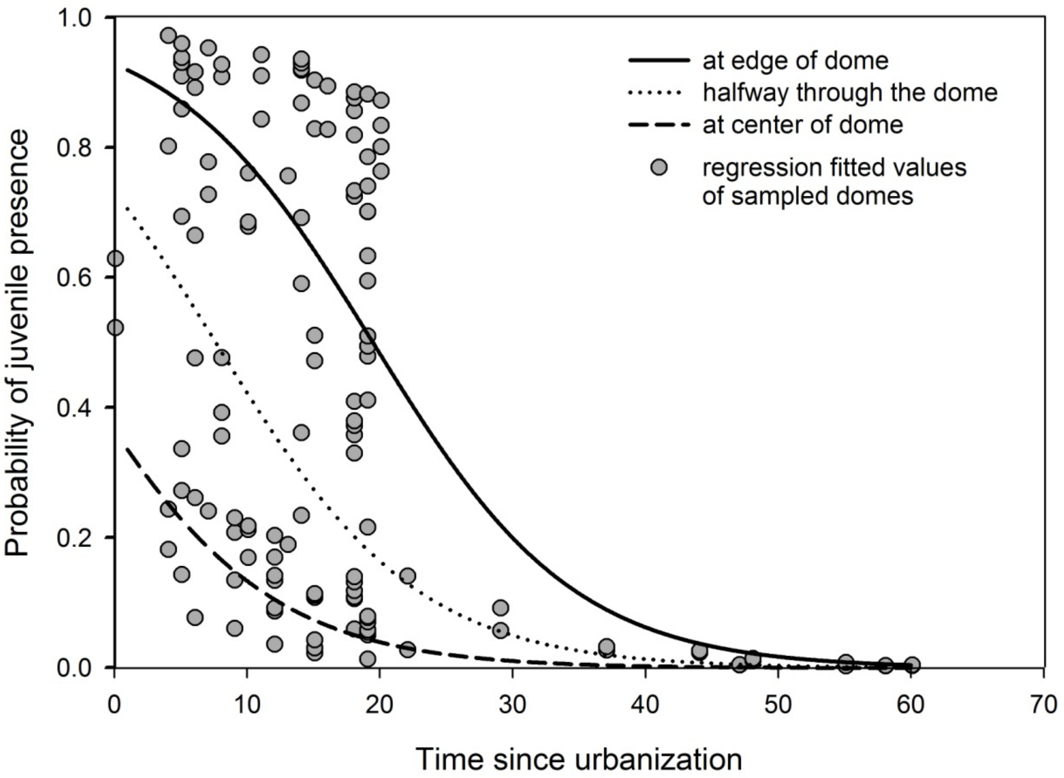

Figure 8. Mixed effects logistic regression model with fitted values of the sampled domes. Juvenile:adult ratio drops significantly around 20 years post-urbanization and is higher at the edge of the dome than in the center.

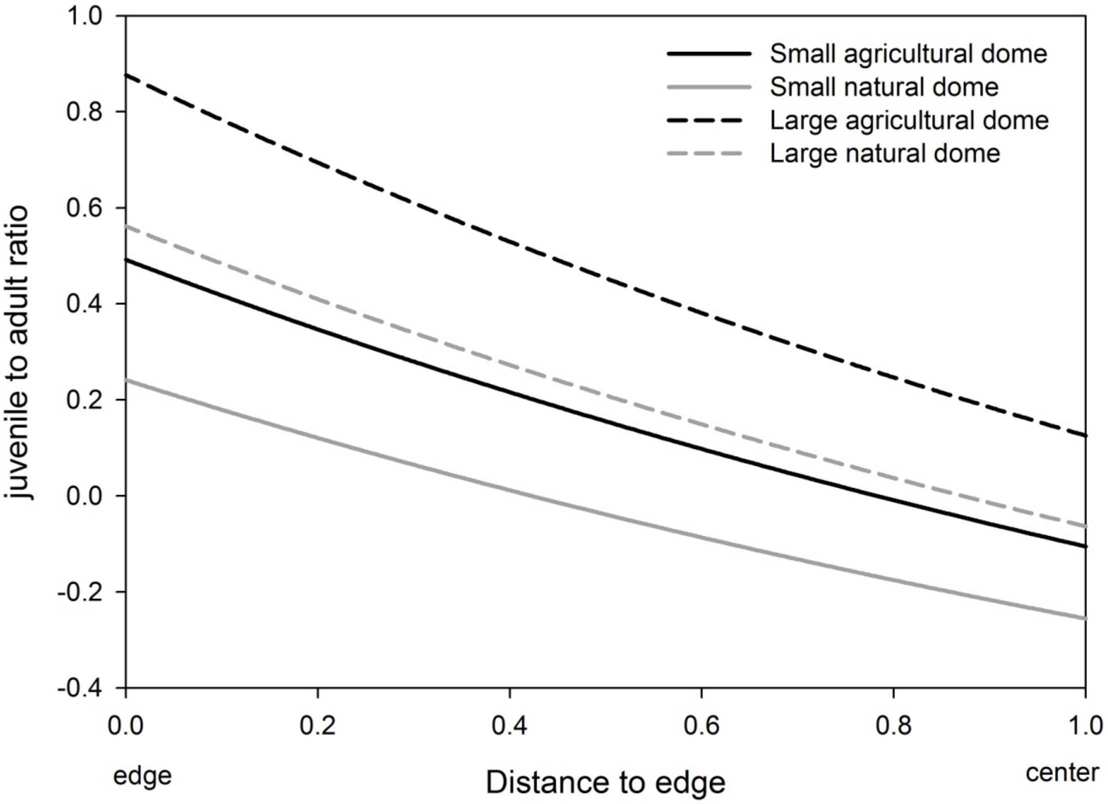

Figure 9. Mixed effects linear regression model of juvenile to adult ratio. Large cypress domes have higher juvenile:adult ratio than small cypress domes. There is higher recruitment in at the edge of the wetland than in the center. Agricultural cypress domes have higher juvenile:adult ratio than natural cypress domes.

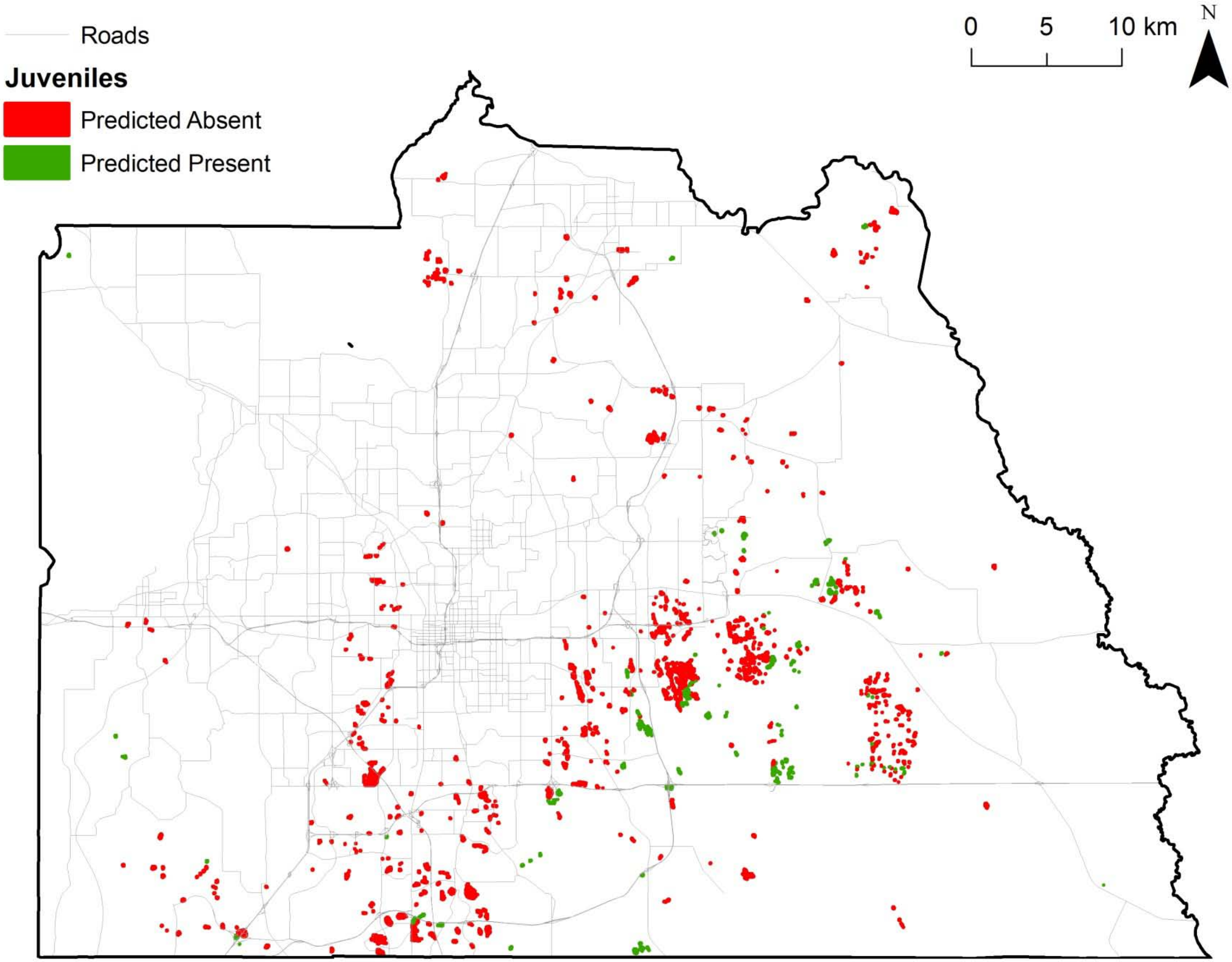

Figure 10. Projected juvenile presence and absence for urban cypress domes. Cypress domes are represented as polygons. Roads represent the more urbanized portions of the study area. Cypress domes that have predicted juvenile presence are on the periphery of the urban area.

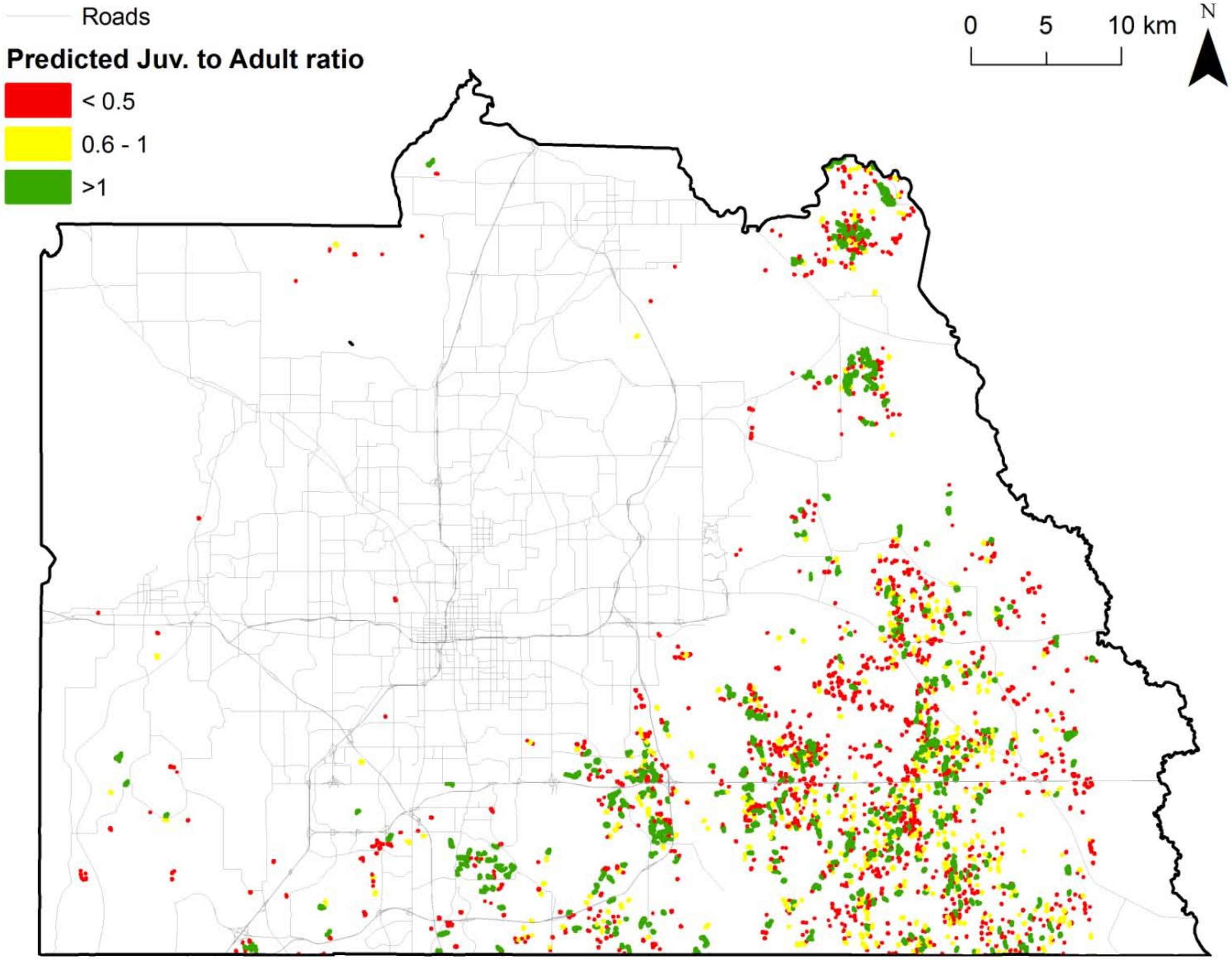

Figure 11. Projected juvenile to adult ratio for natural and agricultural cypress domes. Cypress domes are represented as polygons. Roads are shown to represent the more urbanized portions of the study area. Cypress domes with low juvenile:adult ratio are intermixed with cypress domes with high juvenile:adult ratio. The highest recruiting cypress domes (green) are the larger cypress domes.

Table 3. Top 5 models for predicting probability of juvenile presence for urban cypress domes in central Florida. Thirty total models were run but only models with weight values greater than 0.025 shown [a]. AIC: Akaike Information Criterion value (lower values indicate better models), log (£): log likelihood, Δ_i : difference between lowest AIC value and AIC_i, w_i : model weight.

Model	**AIC**	$\mathbf{\Delta_i}$	**log(£)**	$\mathbf{w_i}$
Distance to edge + Time since urbanization	150.10	0.000	1.000	0.425
Vegetation index + Distance to edge + Time since urbanization	151.70	1.600	0.449	0.191
PCA Axis 2 + Distance to edge + Time since urbanization	152.00	1.900	0.387	0.164
Vegetation Index + PCA Axis 2 + Distance to edge + Time since urbanization	153.40	3.300	0.192	0.082
Time since urbanization	154.30	4.200	0.122	0.052

[a] Relative variable importance of all models: Time since urbanization: 0.988, distance to edge: 0.893, PCA Axis 2: 0.287, vegetation index: 0.037, area of cypress dome: 0.028

Table 4. Top 5 models for predicting juvenile to adult ration in natural and agricultural cypress domes in central Florida. Fifteen total models were run but only models with weight values greater than 0.02 shown.[a] AIC: Akaike Information Criterion value (lower values indicate better models), log (£): log likelihood, Δ_i : difference between lowest AIC value and AIC_i, w_i : model weight.

Model	**AIC**	$\mathbf{\Delta_i}$	**log(£)**	$\mathbf{w_i}$
PCA Axis 1 + distance to the edge + Dome area	-33.64	0	1	0.42
Distance to the edge + Dome area	-32.11	1.53	0.47	0.20
PCA Axis 1 + vegetation index + distance to the edge + Dome area	-31.66	1.98	0.37	0.16
Vegetation index + distance to the edge + Dome area	-30.48	3.16	0.21	0.09
PCA Axis 1 + Dome area	-29.25	4.39	0.11	0.05
Dome area	-28.72	4.92	0.09	0.04

[a] Relative variable importance of all models: Area of cypress dome: 0.986, distance to edge: 0.881, PCA Axis 1: 0.656, vegetation index: 0.267

Table 5. Projections of recruiting cypress domes in central Florida through 2064.

	In 2004		**In 2104**	
	total remaining	total recruiting	total remaining	total recruiting
Natural	891	576	28	18
Ag	1189	769	219	142
Urban	730	115	206	4
Total	**2810**	**1460**	**453**	**164**

Conversion calculations: 25.8% of natural converted to urban, 3.1% of agricultural converted to urban; Loss calculations: 24.2% of natural lost, 25.6% of agricultural lost, 39.2% of urban lost; Recruitment calculations: 64.7% of natural/agricultural recruiting (based on sampling) & 15.7% of urban domes newer than 20 years recruiting (based on predictions), no urban domes older than 20 years recruiting.

APPENDIX C: CHAPTER 4 FIGURES AND TABLES

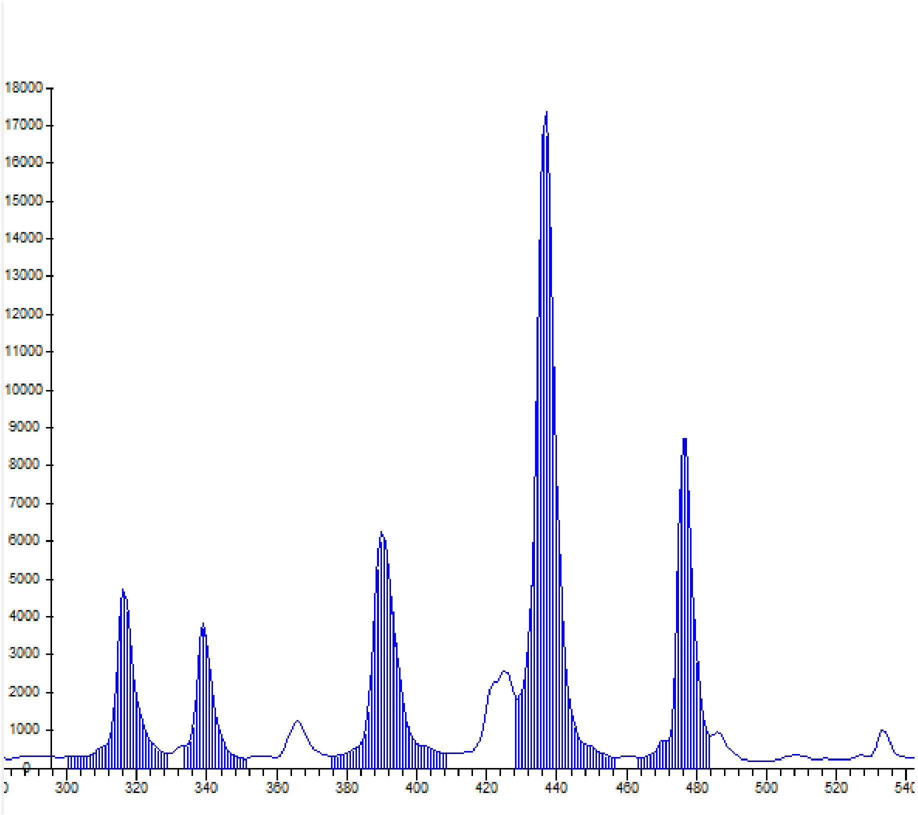

Figure 12. An example of an electropherogram showing 5 alleles at one locus.

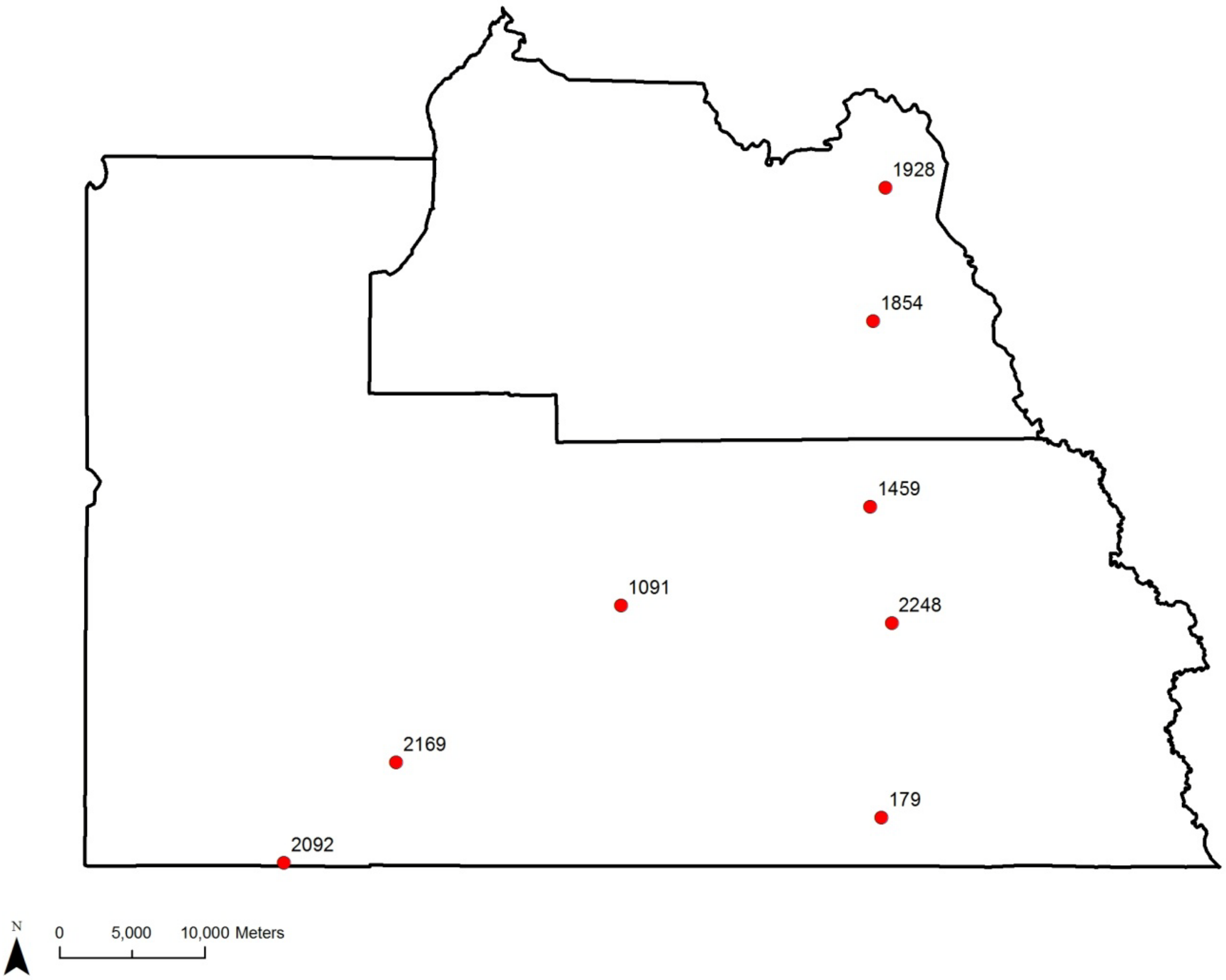

Figure 13. 8 populations analyzed for preliminary genetics analyses.

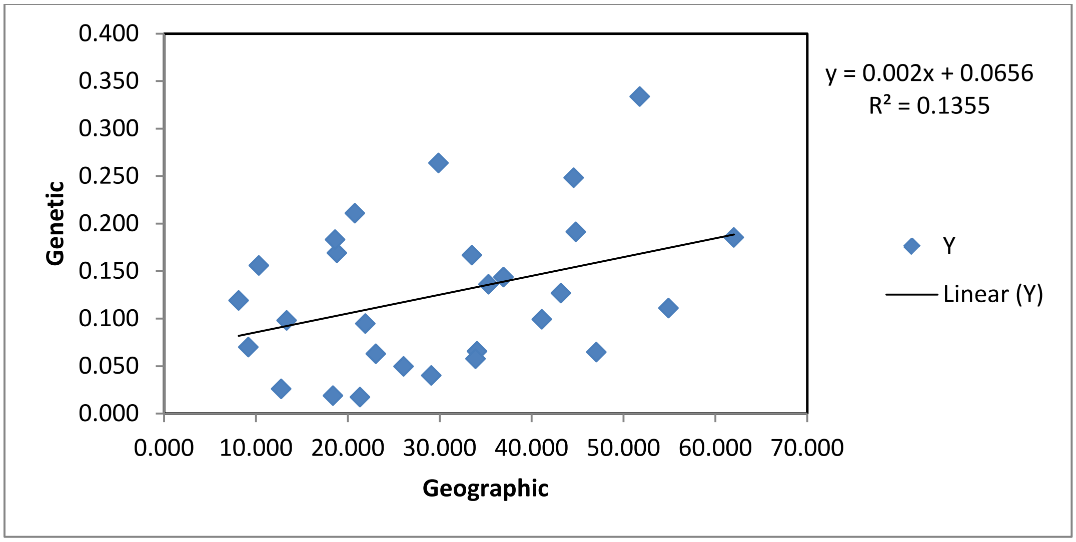

Figure 14. Mantel test on pairwise genetic distances from 8 of the 21 populations. This shows there is very little evidence of isolation by distance.

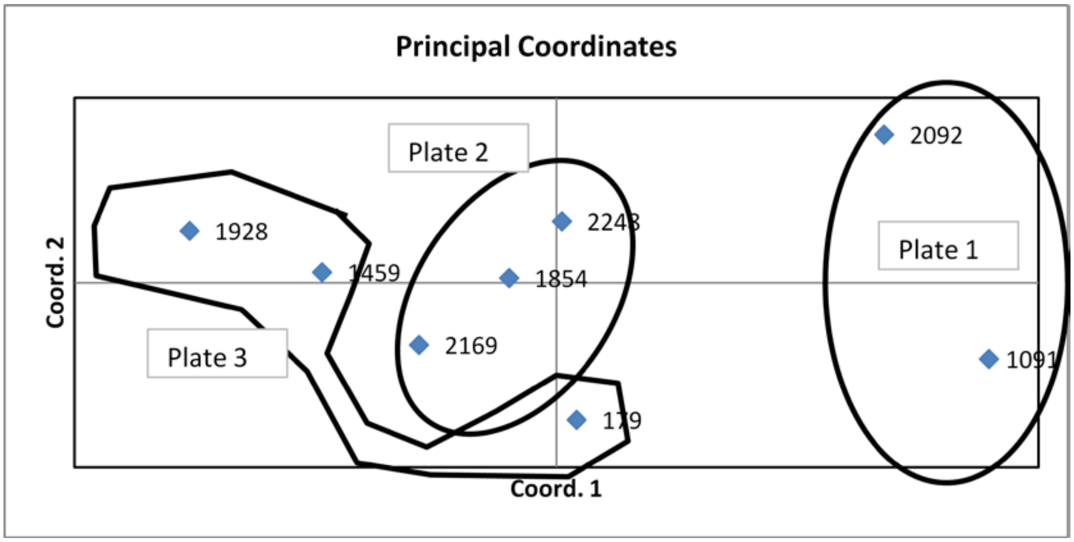

Figure 15. Principal Coordinate Analysis (PCA) of pairwise genetic distances in 8 of the 21 populations. This shows that the populations are most closely related to other populations in the same plate.

Table 6. Results from regular AMOVA showing genetic differentiation among and within populations. Φpt, is the correlation between individuals within a population relative to that of individuals from the whole data set. Number of migrants, Nm = 0.25(1 – Φpt)/Φpt

	df	Percentage
Among populations	7	13%
within populations	247	87%
ϕ_{pt}	0.135	
N_m	1.604	

Table 7. Φpt and geographic distances between 8 of the 21 populations. ΦPT Values below diagonal. Geographic distances above the diagonal.

	2248	2169	1854	1459	1928	179	1091	2092
2248	0	35,312.12	20,770.12	8,118.80	29,871.50	13,345.26	18,616.37	44,815.59
2169	0.063	0	44,583.85	36,946.72	51,771.00	33,506.70	18,814.36	10,319.75
1854	0.017	0.019	0	0.01	9,175.80	34,062.55	26,070.96	54,902.12
1459	0.066	0.050	0.026	0	21,909.41	21,324.39	18,386.41	47,047.26
1928	0.127	0.058	0.095	0.070	0	43,195.91	33,901.83	62,009.35
179	0.099	0.040	0.065	0.111	0.185	0	23,050.06	41,114.10
1091	0.167	0.169	0.144	0.248	0.334	0.156	0	29,087.88
2092	0.098	0.183	0.119	0.211	0.264	0.191	0.136	0

Table 8. Results from Bayesian AMOVA in 8 of the 21 populations.

Model	Dbar	Dhat	pD	DIC	*f*	$\theta^{(I)}$	$\theta^{(II)}$
Full	2024.43	1944.01	80.4135	2104.84	0.693	0.018	0.003
					0.158 - 0.989*	0.011-0.028*	0.0003-0.006*
f -free	2029.66	1772.67	256.988	2286.65	0.494	0.027	0.014
					0.026-0.975*	0.017-0.041*	0.007-0.025*
f = 0	2024.55	1940.83	83.7208	2108.28	-	0.012	0.002
						0.007-0.018*	0.0003-0.004*
θ = 0	2058.22	2000.48	57.7446	2115.97	0.971	0.028	-
					0.894-0.999*	0.018-0.043*	

DIC, deviance information criterion; Dbar, measure of how well the model fits the data; Dhat, measure of how well the best point estimate fits the data; pD, indicates the complexity of the model (approximate number of parameters being estimated). ***f***, the inbreeding coefficient within populations (F_{IS}); $\theta^{(I)}$ and $\theta^{(II)}$, the analogues of F_{ST} and Nei's G_{ST}, respectively; an asterisk denotes upper and lower bounds of the 95% confidence interval.

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