

Connectivity and Change in Oak-dominated Forests

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DISSERTATION

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SUMMARY

My dissertation focuses on major concerns of oak-dominated ecosystems. This includes both oak ecosystems in the western US and eastern and Midwestern regions. Specifically, I examine functional connectivity and barriers to gene flow in valley oak populations in California and address threats to forest diversity and resilience such as fire suppression, biotic invasion. In addition, I examine the effect of management and restoration practices on forest communities, especially red and white oaks in the Chicago metropolitan area. The summary of chapters is provided in chapter one.

In the second chapter, I examined whether certain landscape features such as topography and land cover are barriers to gene flow among valley oak populations, a threatened species in California, U.S.A. Using mathematical equations and GIS, I created landscape resistance surfaces. In addition, I measured recent migration rates among populations to examine the direction of gene flow. The results showed elevation played a greater role in inhibiting gene flow whereas there was no relationship between genetic distances and land cover. I concluded that valley oak restoration and protecting the gene donor populations are crucial for the species conservation.

In the third chapter, I studied woody species community change, non-native species richness over time, and biotic homogenization in urban forests in DuPage County, Illinois. Also, I examined the role of fire, clearing, and deer control management on non-native and shade-tolerant species. The results showed change in the woody species communities over 35 years but no evidence of homogenization. Non-native species richness increased over time, although it was lower in the managed plots. I found that deer control was associated with lower non-native species abundance and richness in year 2014 and suggest that fire prescription and clearing may be more effective in controlling non-native species when applied regularly.

SUMMARY (continued)

In the last chapter, I projected the effect of different management scenarios including deer control, fire prescription, fire and deer control coupled, and no management on oak density and dominance over 100 years. I also used simulations to find expected change in structure and composition of oak dominated forest. The results showed that the importance value of red and white oak will not differ under different management scenarios. Nevertheless, importance value of oaks are related to their longevity and not successful recruitment. Thinning and clearing along with prescribed fire and deer control may be more effective in oak restoration in the Midwest.

CHAPTER ONE

1. INTRODUCTION

1.1. Why study oak-dominated forests?

This dissertation is about oaks. The oak genus (*Quercus*) is the most diverse woody group in North America and has been a dominant component of eastern forests for millennia (Hanberry and Nowacki 2016). Oaks provide a range of ecosystem services, such as high-quality timber, food and habitat for wildlife, recreational areas, watershed protection, and possibilities for adaptation of forest management to climate change (Löff et al. 2016). Given their abundance and longevity, the ecological services they provide prevail longer than other woody species (Cavender-Bares 2016). For example, the U.S. Forest Service estimates that oaks sequester more carbon than any other woody group in the continental U.S. (data provided by Chris Woodall, US Department of Agriculture, Forest Service, Northern Research Station). Furthermore, habitats created by oaks can persist for centuries due to the long lifespan of individual trees and the durability of the deadwood (Ellison et al. 2005). Oak is, therefore, one of the most important tree genera for endangered invertebrates (Tallamy and Shropshire, 2009), lichens, fungi (Thor et al. 2010), and birds (Rodewald and Abrams, 2002).

Oak forest types comprise half of the forest lands in the eastern U.S. (Oswalt et al 2014) and are an important component in the west. Yet, over the past decades, anthropogenic drivers have been linked to shifts in community structure and composition of oak ecosystems (e.g., McEvan et al. 2011; Harrington and Devine 2006). Some of the main drivers of change in oak-dominated forests include fire suppression, biotic invasion, and land-use change leading to lack of gene flow among oak populations. Fire suppression may lead to the replacement of fire-

stabilized oaks by fire-sensitive species, mainly shade-tolerant species (Nowacki and Abrams, 2008). This process is called mesophication and is one of the major changes in oaks forests in the eastern U.S. in recent decades (McEwan et al. 2011; Nowacki and Abrams, 2008). Similarly, non-native species may compete with oak and other native species and produce substantial changes in natural ecosystems (McKinney and Lockwood, 1999). As a result, fire suppression and an increase in non-natives may lead to biotic homogenization (McKinney and Lockwood, 1999; Hanberry et al. 2012), a threat to biodiversity (Blair 2001).

Another threat to oak ecosystems is land use change that may impede gene flow among oak populations (Grivet et al. 2008). Limited gene flow may decrease populations' resilience, especially when they are small (Frankham 2006). Maintaining gene flow among populations conserves genetic diversity required for evolutionary adaptation in the long-term (Frankham et al. 2002). Therefore, quantifying the degree to which a landscape promotes or hinders movements (seeds, pollen, etc.) among patches of habitat is essential to conservation management decisions (Calabrese and Fagan 2004).

Management techniques are often applied to counteract the homogenization of forests. These management activities include fire prescription, understory thinning, and deer control. Here I summarize how each of these practices can be influential to oak ecosystems. Managers use fire to promote the establishment and growth of fire-adapted oaks (Vander Yacht et al. 2017). Moreover, fire can control competition from shade-tolerant and non-native species in the forest understory (Nuzzo 1991; Keyser et al. 2017). Fire stimulates germination, prepares suitable seedbed conditions, removes excessive litter, and retards woody species dominance, thus ensuring adequate light in the understory (Dey and Kabrick 2015). However, the constant

increase of shade tolerant species may decrease flammability of forests (Babl et al. 2020), making prescribed fire less effective

Deer can have an immediate impact on forest health and diversity by reducing the abundance of oaks (Rooney and Waller 2003) and increasing invasive plants (Fisichelli et al. 2013) through selective browsing. Some studies show that recovery of local plant populations began quickly after deer exclusion (Shelton et al 2014; Owings et al 2017). However, deer control may not be as effective in maintaining native species if the area has been heavily browsed (Nuttall et al. 2014). In that case, more intensive treatments focused on canopy structure, such as mechanical canopy thinning and understory clearing that target shade-tolerant and non-native species, are often necessary to promote an oak canopy (Iverson et al 2008; Dey et al. 2010).

Scientifically, oaks provide a model clade for the study of many disciplines from genes to communities to landscapes. Given that oaks are often ecologically dominant, discoveries related to oak gene flow will be relevant at the ecosystem level and can inform management in the face of threats from global change (Gailing et al. 2009; Gugger et al. 2016; Sork et al. 2016). Influences of geological history that lead to landscape features, such as mountain ranges, represent evolutionary legacy effects. Understanding how these features have shaped gene flow among populations can help explain the diversity, composition and function of ecosystems we observe today (Cavender-Bares 2019).

In this dissertation, I use oaks as an important model system to study community dynamics and landscape genetics. Specifically, I have tried to address some major concerns about oak-dominated ecosystems, including oak ecosystems in both the western U.S. and eastern and Midwestern regions. Furthermore, I have successfully developed a model that predicts

connectivity and community composition change throughout time. These projections are made either directly by a simulation model or by inference using observed trends. My ultimate goal is to examine the current status and long-term changes in oak-dominated forests to inform forest managers and landscape planners and ensure oak resilience in the future. Below, I provide an overview of each my dissertation chapters within a conservation context.

1.2. Summary of chapters

1.2.1. Chapter Two: Effects of landscape features on gene flow of valley oaks

(*Quercus lobata*)

Factors facilitating or inhibiting habitat connectivity affect gene flow and, consequently, long-term persistence among populations. However, these factors are largely unknown for most species. Specifically, there have been conflicting reports as to whether the arid flats of California's Central Valley are a barrier to gene flow in valley oak populations (Grivet et al. 2008; Sork et al. 2016). In this chapter, I examined whether certain landscape features such as topography and land cover prohibit gene flow among valley oak populations, a threatened species in California, U.S.A. I used GIS to create different resistance surfaces between each oak population, based on intervening land cover type and topography. Also, I measured recent migration rates among populations to test whether there are more “north-south” than “east-west” links and whether gene flow corresponds to topographic and land cover barriers.

The results showed a relationship between genetic distances and elevation but no relationship between genetic distances and land cover. I concluded that high elevations in the northern and central regions of the valley oak range restrict gene flow, whereas both high elevation and low elevation features (such as the central valley itself) restrict gene flow in the

southern range of the species. There was greater gene flow in the north-south direction, compared to gene flow in the east-west direction. The limited links between the east-west populations may be related to higher connectivity in the northern Central Valley. As a result, I predicted that southern populations of valley oak may become more differentiated due to genetic isolation and local adaptation, especially considering the impact of climate change. A long-term connectivity plan to restore valley oaks throughout their historical range, especially in mid-elevation areas, would be particularly valuable for the conservation of the species. These results help infer the impacts of natural and anthropogenic landscape barriers, identify the most vulnerable populations, develop regional conservation priorities, and predict future response to environmental change.

1.2.2. Chapter Three: Community change in urban forests of the Midwestern U.S.

Urban forests constitute one of the most significant assets of a city (Elmqvist et al 2013). However, they are declining nationally at a rate of about 4 million trees/year (Nowak et al. 2013). As many forest transitions occur close to urbanizing areas, remaining forests may experience high levels of fragmentation, invasion of non-native species (González-Moreno et al. 2013), and mesophication due to fire suppression. Maintaining forest quantity and quality in the face of increasing urbanization is therefore a pressing global challenge. In this chapter, I used long-term (35 years) empirical data to examine community change, trends in non-native species over time, and biotic homogenization in oak-dominated forests in DuPage county, Illinois. In addition, I examined the role of ongoing management (fire, and deer control, and understory clearing) on controlling the non-native and shade-tolerant species.

The results showed a change in the woody species community over 35 years but no evidence of homogenization. Non-native species richness increased over time, although it was lower in the managed plots. There were also some trends toward higher shade-tolerant species richness and lower specialist richness over time. Deer control had a positive effect on controlling non-native abundance and richness. Overall, the vegetation management in the plots did not prevent non-native species increase over time. We suggest that if prescribed fire and clearing were more consistent (i.e., repeated at regular intervals) it might have been even more effective in controlling the non-native species. Our work contributes unique insight into long-term forest management and plant invasions in an urban landscape.

1.2.3. Chapter Four: Modeling the effects of fire prescription and deer control on oak dominance in urban forests of the Midwestern USA

Restoring oak woodlands and other natural communities is a management priority in the U.S. (Dey et al. 2017). Some studies predict that, without effective restoration programs, white oak may nearly disappear in many of the remaining upland forest tracts within the next 50 to 100 years (Fralish 2004, Haas and Heske 2005) and be replaced by sugar maple and other shade-tolerant species. Long-term empirical data on restoration and management impacts are rare. Therefore, models that project long-term management effects are essential to see overall trends in forest composition and structure. In this study, I used the DuPage County empirical data (described above) along with model simulations to explore the management activities that maintain oaks and control the spread of oak competitors, especially sugar maple, over the next 100 years. Management scenarios included deer control every year, fire prescription every three years, fire and deer control coupled, and no management. I examined how forest characteristics like species richness, basal area, canopy cover, and number of mature trees and dominance of

oaks and other tree species changed over 100 years in different management scenarios. In addition, I calculated the importance value of oaks and other common species to represent relative density and dominance.

The results suggest that the importance value of red and white oak will not differ under different management scenarios. Fire combined with deer control may reduce sugar maple importance value compared to the no management and deer control scenario. However, sugar maple importance value will continue to increase under all management scenarios throughout time. Structural changes include a decrease in stem density and an increase in basal area over the simulation period. Simultaneously, species richness may decline over time. Analysis of diameter classes shows that the high importance of oaks is mainly due to the species' longevity and not added recruitment. Consequently, when the current mature oak trees die off, there is a high chance that sugar maples will replace them because of their successful recruitment and understory dominance. Hence, there is a critical need for the removal of large sugar maple trees mechanically via thinning and cleaning to create a more oak-friendly environment.

1.3. Recommendations for improving functional connectivity and restoration in oak-dominated forests

A long-term plan to restore oak ecosystems throughout their historical distribution is beneficial for both ensuring functional connectivity and maintaining oak dominance. Conservation strategies that ensure gene flow among populations should include restoring suitable habitat for oaks across the habitat range of oak populations. Prescribed fires are important restoration tools but not sufficient to improve oak dominance in our region. Increasing the intensity of fire may lead to the death of midstory species but is unlikely to reduce larger

trees that contribute widely to shade conditions (Lettow et al. 2014). Therefore, prescribed fire incorporated with other restoration practices such as thinning to mimic historic disturbances that once promoted oak natural communities (e.g. savannah, woodland, forest) can be effective. Finally, non-native species can threaten oak sustainability (Schulte et al 2011). Non-native species control would not be fully effective in a developed landscape unless it is extended to the neighboring environments (e.g., residential areas, city parks, street trees), so a collaborative public-private approach would be necessary (Webster et al. 2006).

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CHAPTER TWO

2. EFFECTS OF LANDSCAPE FEATURES ON GENE FLOW OF VALLEY OAK (*QUERCUS LOBATA*)

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Gharehaghaji, M., Minor, E.S., Ashley, M.V., Abraham, S.T. and Koenig, W.D., 2017. Effects of landscape features on gene flow of valley oaks (*Quercus lobata*). *Plant ecology*, 218(4), pp.487-499.

2.1. Abstract

Landscape features affect habitat connectivity and patterns of gene flow and hence influence genetic structure among populations. We studied valley oak (*Quercus lobata*), a threatened species of California (USA) savannas and oak woodlands, with a distribution forming a ring around the Central Valley grasslands. Our main goal was to determine the role of topography and land cover on patterns of gene flow and to test whether elevation or land cover form stronger barriers to gene flow among valley oak populations. We sampled valley oaks in 12 populations across the range of this species, genotyped each tree at eight nuclear microsatellite loci, and created a series of resistance surfaces by assigning different resistance values to land cover type and elevation. We also estimated recent migration rates and evaluated them with regard to landscape features. There was a significant but weak relationship between Euclidian distance and genetic distance. There was no relationship between genetic distances and land cover, but a significant relationship between genetic distances and elevation resistance. We conclude that gene flow is restricted by high elevations in the northern part of the valley oak range and by high elevations and the Central Valley further south. Migration rate analysis

indicated some gene flow occurring east-west but we suggest that the high connectivity in the northern Central Valley is facilitating the formation of these links. We predict that southern populations may become more differentiated in the future through genetic isolation and local adaptation taking place in the face of climate change.

2.2. Introduction

Landscape features and topography affect habitat connectivity and gene flow and thus influence genetic structuring of populations at a regional level (Gomez et al. 2005). Reduced connectivity and gene flow can decrease the resilience, adaptability, fitness and fertility of populations, especially when populations are small (Frankham 2006). Despite the clear importance of habitat connectivity for population persistence, factors facilitating or inhibiting connectivity are largely unknown for most species.

Landscape genetic approaches offer powerful tools for explicitly quantifying the effects of landscape features on spatial genetic variation (Holderegger and Wagner 2008; Balkenhol et al. 2009), but landscape distance/resistance studies are less common in the study of plant systems compared to animals (Holderegger et al. 2010; Storfer et al. 2010). Examples include studies on Arkansas valley evening primrose (*Oenothera harringtonii*, Rhodes et al. 2014) and Engelmann oak (*Quercus engelmannii*, Ortego et al. 2012), both of which found that isolation by distance (IBD) and topographic features, especially elevation, have a significant effect on genetic patterns. Cushman et al. (2014) identified rivers and streams as landscape features that influence genetic structure and restrict gene flow of Fremont cottonwood (*Populus fremonti*), but isolation by distance was not detected in their study. A recent study by Ortego et al. (2015) on canyon live oak (*Quercus chrysolepis*), a species whose distribution is divided by California's Central

Valley, found that genetic distance was highly correlated with geographical distance and identified habitat stability as the primary driver of population genetic differentiation. Their study reported little genetic differentiation between populations from either side of the Central Valley.

The pronounced ecological gradients and complex climatic and geological history of California has produced one of the most geographically-complex patterns of genetic diversity on Earth (Raven and Axelrod 1978; Calsbeek et al. 2003; Davis et al. 2008). As a result, the California biota offers an excellent opportunity to study landscape features and their relation to observed patterns of genetic diversity. Oak woodlands and savannas make up nearly a quarter of California's forests and woodlands (Davis et al. 1998). California's oak landscapes have been a recurrent focus of conservation attention due to concerns about habitat conversion to farmland, vineyards, and other land uses, arrival and spread of invasive diseases such as sudden oak death syndrome (SOD), poor regeneration (Zavaleta et al. 2007), and climate change. Such factors can result in surviving populations being genetically structured and effectively isolated (Sork et al. 2010). Understanding how environmental and landscape-level features influence genetic variation and structure in these oaks will help us identify specific barriers to dispersal and corridors that facilitate gene flow, enabling improved prediction of the impact of future changes to the landscape (Schwartz et al. 2009).

Valley oak (*Quercus lobata*) is an ecologically important species endemic to California savannas and oak woodlands. Due to its propensity to occupy locations that are desirable for farmlands, ranches, vineyards, and suburban developments, valley oak has lost more of its habitat than any other oak species in California (Pluess et al. 2009; Whipple et al. 2011; Ashley et al. 2015). For example, it occupies 5% of its historical range in San Joaquin Valley (Kelly et al. 2005). Alterations in the structure and distribution of valley oak stands could affect main

avian dispersers of the species, acorn woodpeckers (*Melanerpes formicivorus*) and California scrub-jays (*Aphelocoma californica*), a host of other species, both vertebrate and invertebrate, that are associated with California oak woodlands, along with rates of soil and landform development (Pavlik et al. 1991; Howard 1992).

Many studies of genetic structure have revealed strong diverged lineages within species across geographic features (Rissler et al. 2006). In California, one important feature is the dry, flat Central Valley. The ranges of dispersal-limited, habitat-specialized species and ones less adapted for the arid conditions are intersected by the Central Valley. Such species include Arthropoda such as *Greya politella* (Brown et al. 1997), mammals, particularly rodents (Maldonado et al. 2001), amphibians such as *Ensatina eschscholtzii* Gray (Wake et al. 1986), *Batrachoseps* (Jockusch et al. 2001) reptiles including *Diadophis punctatus* (Feldman 2000), and several species of oaks, genus *Quercus*.

While Grivet et al. (2006) hypothesized that the geological history of California is a primary driver of the current genetic structure of oak populations and that oak populations have been less strongly affected by past climatic changes such as the Last Glacial Maximum (LGM), Sork et al. (2010) and Gugger et al. (2013) showed that genetic variation in valley oak is significantly correlated with climatic variation and LGM climate. On the other hand, Lancaster and Key (2013) have shown that California's topographic complexity and geographical location are critical for plant species persistence and diversification, whereas its temporary climatic conditions have been less important.

There are conflicting reports as to whether the arid flats of California's Great Central Valley are in fact a barrier to gene flow. Previous studies on valley oak (Grivet et al. 2007; Sork

et al. 2010; Gugger et al. 2013) report genetic differentiation among valley oak populations in the inland foothills of the Coastal Range and the western foothills of the Sierra Nevada, with higher gene flow north-to-south along climatically similar mountain corridors than east-to-west across the Central Valley. These findings suggest a role for environmentally mediated historical vicariance and that the Central Valley may be a barrier to gene flow in this species. Prior studies indicating that geographical barriers, possibly combined with climatological changes, may have affected the Californian fauna and flora include Calsbeek et al. (2003) and Lapointe and Rissler (2005). In contrast, Grugger et al. (2016) and Sork et al. (2016) failed to observe any clear east–west structure in valley oaks using candidate genes. Here we explicitly test if topographic features are a barrier to gene flow in valley oak by creating resistance surfaces.

Elevation is but one of the factors likely to correlate with environmental variables important in the ecology of oak species (Thomassen et al. 2010). Land use change also threatens to reduce valley oak genetic diversity and evolutionary potential (Grivet et al. 2008). We hypothesize that different land cover influences genetic structure. In particular, woodland and mixed forest that are typical habitats for valley oaks, and to a lesser extent grassland and oak savannah, allow for pollen and seed dispersal by acorn dispersers e.g. scrub jays and therefore, should facilitate gene flow, whereas shrubland, urban and non-vegetated land cover should inhibit it.

Here we extend a recent study by Ashley et al. (2015), who, along with others (Grivet et al. 2008; Sork et al. 2010) suggested that California’s Central Valley and other topographical features including the Coast Ranges and the Sierra Nevada mountains are barriers to gene flow in valley oak. Our aim was to disentangle the effect of distance and landscape features such as elevation and land cover on the observed pattern of genetic variation of valley oak populations.

We predicted that isolation by resistance (IBR) with different resistance values assigned to land cover types and elevation would better explain genetic variation than isolation by distance (IBD). In addition, we measured recent migration rates among populations to test whether there are more north-south than east-west links and whether gene flow is matched to topographic and land cover barriers.

2.3. Methods

2.3.1. Study species

Valley oak is the largest North American oak, with trees standing 10-25 m tall and 0.5-0.7 m diameter at breast height (Munz 1973). It is wind pollinated and its seeds are dispersed by birds and rodents (Grivet et al. 2005; Pesendorfer et al. 2016). Studies of historical and contemporary gene flow indicate that the scale of pollen and seed dispersal in some populations is on the range of 100–300 m, which allows opportunity for adaptation to local environmental conditions (Pluess et al. 2009; Sork et al. 2010). Valley oak habitat is found in the lower elevations of the central and northern Coastal Ranges and the Sierra Nevada mountains and forms a ring around Central Valley grasslands (Figure 1). The density of valley oaks varies widely, from closed-canopy forests in some regions to open savannahs in drier parts of their range.

California's Central Valley covers approximately 155,000 km² of land or nearly 40% of the total land area of the state. On average, it is about 725 km long and 80 km wide, is primarily agricultural, and is often in a state of moderate to severe drought (Whiteside 2007). It is also home to 588 rare and endangered species, more than any other region in the continental United States. The rapidly growing population of the Central Valley has caused the loss, degradation

and fragmentation of habitats through the development of agricultural and urban areas (Hosley et al. 2012). Scattered valley oaks occur in the Central Valley but are relatively uncommon due to agricultural development and loss of riparian habitat.

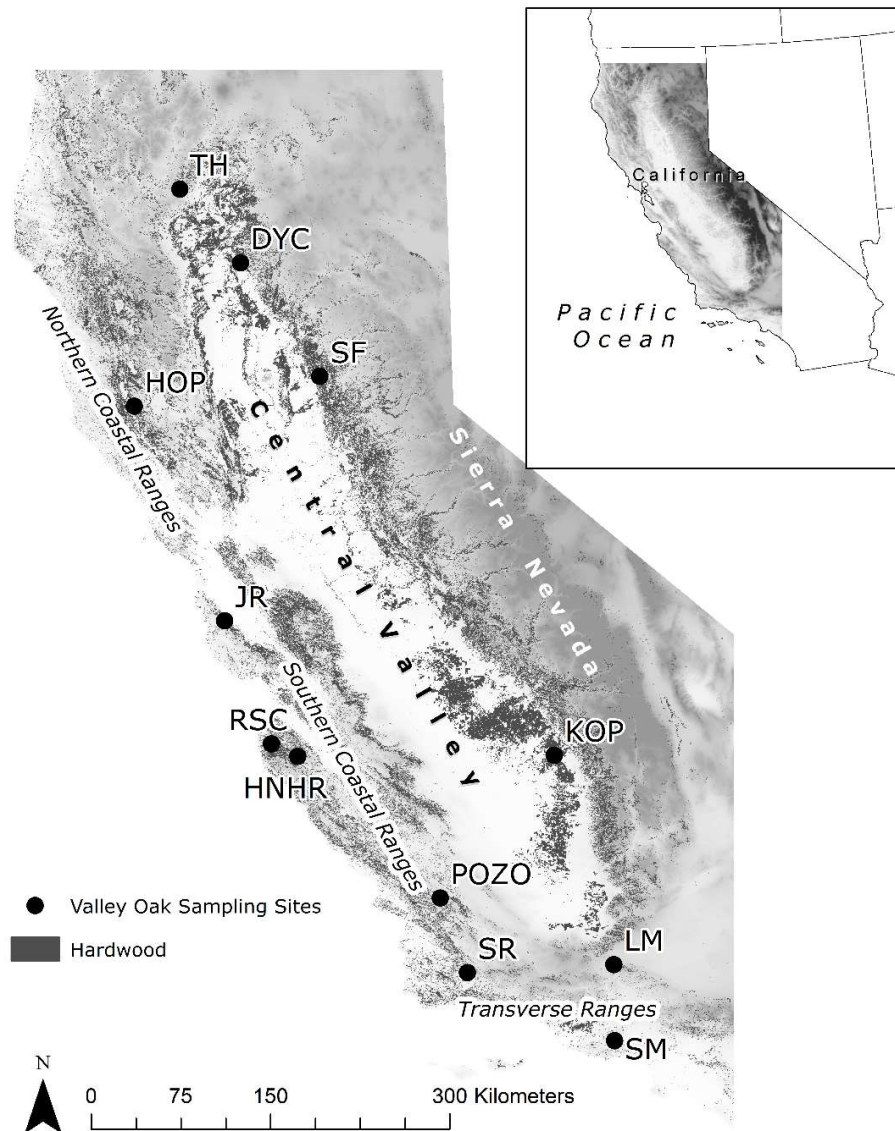


Figure 1. Valley oak sampling sites across hardwood forest (*Quercus lobata*) (USDA, 2011): Tower House, Shasta (TH), Dye Creek Reserve, Tehama (DYC), Sierra Foothills Station, Yuba (SF), Kaweah Oaks/River Preserve, Tulare (KOP), Liebre Mountain, Los Angeles (LM), Santa Monica Mountains, Ventura (SM), Sedgwick Reserve, Santa Barbara (SR), Pozo, San Louis (POZO), Hastings Reservation, Monterey, (HNHR), Rancho San Carlos, Monterey (RSC), Jasper Ridge, San Mateo (JR), Hopland Research Station, Mendocino (HOP).

2.3.2. Genetic data

Leaf tissue was collected from 270 trees in 12 populations spread across most of the species' range (Fig. 1). Samples were genotyped at eight nuclear microsatellite loci. The eight loci used were highly variable, with an average of 8.12 alleles per locus (Ashley et al. 2015). Sampling sites and microsatellite genotyping are described in more detail by Ashley et al. (2015).

Ashley et al. (2015) calculated genetic differentiation statistics including Nei's (1973) multiallelic estimate of F_{ST} and D_{JOST} (Jost 2008) using the R (R Development Core Team, 2014) package *diveRsity* (Keenan et al. 2013) and these were used as measures of genetic distance in this study. D_{JOST} (Jost 2008) measures the fraction of allelic variation among populations and overcomes the problem that F_{ST} is limited to low values when heterozygosity is high. However, D_{JOST} can be biased upwards. We therefore used both following the recommendation of Whitlock (2011).

2.3.3. Landscape analysis

To measure isolation by distance, we computed the pairwise straight-line (Euclidean) distances between valley oak stands in GenAlEx (Peakall and Smouse 2012). To measure IBR, we modeled landscape resistance as a function of land cover and elevation. We generated multiple resistance grids in ArcGIS 9.3 (Esri, 2014) in which each grid cell was assigned a value based on the hypothesized resistance of gene flow to the land in that cell.

As a precursor to the resistance grids, we first created a land cover raster by combining two GIS datasets. The most recent CALVEG land cover dataset from 2011 (30 x 30 m resolution), originally created by USDA Forest Service (1981), includes detailed vegetation

classification including valley oak habitat but does not cover the entire study region. Therefore, we filled in areas with no CALVEG coverage with the USGS GAP Land Cover data. By combining the two datasets, we created a 30 x 30 m land cover map with seven land cover types (Table I). We used Shuttle Radar Topographic Mission (SRTM) data for elevation, which is available in 3 arc second intervals (~ 75m resolution in our study region).

To identify the optimum resistance values for elevation and land cover, we used the model optimization approach introduced by Cushman et al. (2006) and refined by Shirk et al. (2010). We related each land cover type and elevation to landscape resistance with a mathematical function (see model functions below) and used each function to reclassify appropriate raster data into a resistance surface. We generated alternative parameter values favoring the direction that increased the correlation until we observed a unimodal peak of support (Shirk et al. 2010).

Table I. RANKING OF COVER TYPES BASED ON EXPERT OPINION INDICATING RELATIVE DEGREE OF RESISTANCE TO GENE FLOW.

Landcover type	Resistance ranking
Valley Oak	1
Hardwood	2
Mixed forest	3
Grassland	4
Shrubland	5
Conifer	6
Non Vegetation (Urban, Water, Barren)	7

For land cover, we first ranked resistance of each land cover type based on expert (M. V. Ashley personal recommendation) opinion about valley oak biology and habitat relations (Table I). Our ranking of habitat was based on resistance or facilitation of pollen flow and seed movement, and in accordance with valley oak favored habitat and occurrence. Second, we reclassified the resulting categorical rank raster according to the function from Shirk et al. 2010:

$$R_i = (Rank_i/V_{max})^x * R_{max} \quad (1)$$

Where R_i = resistance value of land cover type i, $Rank_i$ is the resistance rank of land cover type i (from Table I), V_{max} = maximum resistance rank (equal to 7, in our case, which was the resistance rank for all non-vegetation cover), x = a shape parameter that informs relative differences in resistance among different cover types, and R_{max} = the maximum resistance value

for any land cover type. We tested five values of R_{max} (5, 10, 25, 50 and 100) and five values of x (0, 0.1, 0.25, 0.5 and 1) and calculated a resistance value for each land cover type for each set of parameters for a total of 25 candidate models. Valley oak habitat was always assigned a resistance value of 0.01. By systematically varying x and R_{max} values, we aimed to find the optimal hypothesis about the effect of land cover on gene flow.

Valley oak grows at higher elevations in the southern part of its range and lower elevations in the northern part (Griffin and Critchfield 1972). Therefore, we divided valley oak habitat range into north and south to account for this apparent geographic division. We tested several different latitudes as the dividing line and settled on 35° 52' 00" latitude as the dividing line between 'north' and 'south' that resulted in the strongest relation between resistance as a function of elevation and genetic variation. No study, to our knowledge, has specifically identified a latitude leading to a disjunction of genetic structure. Grivet (2007) and Ashley et al (2015), however, found that the western and eastern populations of valley oak differ genetically at the northern and southern ends of its range.

We then reclassified the digital elevation model according to an inverse Gaussian function.

$$R = R_{max} + 1 - R_{max} * e^{\frac{-(\text{elevation} - E_{opt})^2}{2 * E_{SD}^2}} \quad (2)$$

Where R_{max} , E_{opt} and E_{SD} represent the maximum resistance, optimal elevation and the standard deviation about the optimal elevation, respectively. Thus, as elevation increases or decreases away from E_{opt} , resistance increases to R_{max} at a rate governed by E_{SD} .

We evaluated three values of R_{max} (5, 10 and 25), three standard deviations (E_{SD}) of 500, 1000, 1500 and five values of E_{opt} in the north (ranging from 0 to 800 m in 200 m increments)

and five values of E_{opt} in the south (ranging from 900 to 1700 m, in 200 m increments) for a total of 45 candidate models of elevation resistance.

We used Circuitscape 4.0.5 (McRae et al. 2013) to measure pairwise landscape resistance among all populations for each landscape resistance scenario. Circuitscape proved to be faster and more efficient compared with the least cost path (LCP) procedure in ArcGIS due to the smaller number of resistance surfaces made compared to LCP. In the LCP method, least cost distance is measured from a given population to each of the other populations in each run whereas in CIRCUITSCAPE all the populations can be given as the input, and thus resistance distance is measured from all population to every other population in a single run. We used a four-neighbor connection scheme to calculate resistance between point locations. Because our land cover map exceeded the maximum number of grid cells that Circuitscape can handle, we aggregated groups of 25 pixels in each land cover resistance surface and groups of four pixels in each elevation resistance surface to create new resistance surfaces with 150 x 150 m pixels whose values reflected the average resistance of the aggregated cells.

We used causal modeling (Legendre and Troussellier 1988) to find the relationships between genetic distance among populations and compared multiple alternative hypotheses of landscape resistance to evaluate the factors that limit gene flow (Cushman et al. 2006). After calculating resistance between each pair of populations for each resistance surface, we used Mantel tests (Mantel 1967) and partial Mantel tests (Smouse et al. 1986) to test the relationship between genetic distance and landscape resistance when removing the effects of Euclidean distance. In all Mantel tests, correlation coefficients for genetic distances were consistently higher for F_{ST} than D_{JOST} . Therefore, we only report results from F_{ST} , which is a basic descriptor

of population structure (Neigel 2002). We identified the most supported model as the one with the highest significant correlation.

Mantel tests have been criticized for their lower power compared to traditional linear models leading to underestimation of the true magnitude of a relationship (Legendre and Fortin 2010). Therefore, we also conducted general linear mixed models (GLMMs), which account for dependency between pairwise observations in a distance matrix (Yang 2004) and are a more robust approach for landscape genetic inference. Before performing a GLMM, we checked collinearity between the explanatory variables. We fitted maximum likelihood population effects (MLPE) models (Clarke et al. 2002; Van Strien et al. 2012) with residual maximum likelihood (REML) estimation using the “lmer” function in the package “lme4” (Bates et al. 2011) for R (R Development Core Team 2011). Pairwise genetic distance (F_{ST}) was used as the dependent variable, while elevation and land cover resistance between populations were the independent fixed variable. We used ANOVA to select the best model.

We explored recent migration rates among the twelve populations using BayesAss 3.0.3 (Wilson and Rannala 2003). BayesAss uses a Bayesian MCMC approach to estimate asymmetric migration over the last two to three generations (Wilson and Rannala 2003). We assessed convergence by using long (10^7) iteration runs with large sampling frequencies (2000), and long (10^6) burn-in periods and by comparing migration rates across 10 replicate runs using different starting seeds, as recommended by the program’s authors (Wilson and Rannala 2003). We examined the results for evidence of convergence by comparing the posterior mean (the matrix parameter of migrational rates) for consistent results (Clark et al. 2013). We set delta values of allele frequency, migration rate and inbreeding to 0.3. Delta is the parameter that defines the size of the proposed change to the parameter values at each iteration (Wilson and Rannala 2003).

2.4. Results

Our landscape modeling results revealed a significant but weak relationship between genetic distance and Euclidean distance ($r = 0.16$, $P = 0.001$). The optimized IBR models provided better support, as both land cover ($r = 0.25$, $P = 0.041$) and elevation ($r = 0.64$, $P = 0.001$) were significantly related to genetic distance (Table II). However, after removing the effect of Euclidean distance with a partial Mantel test, land cover resistance was no longer significantly related to genetic distance (Mantel $r = 0.23$, $P = 0.76$). Furthermore, there was no strong unimodal peak for any of the land cover resistance models (Figure 2). In contrast, the Mantel correlation between resistance as a function of elevation and genetic distance remained high after removing the effect of Euclidean distance ($r = 0.63$, $P = 0.001$). The optimum elevation resistance model included a maximum resistance (R_{max}) of 25, an optimal elevation (E_{opt}) of 200 m in the north and 1100 m in the south and a standard deviation about the optimal elevation (E_{SD}) of 500 (Figure 2)

Table II. MANTEL CORRELATIONS BETWEEN THE MOST HIGHLY SUPPORTED RESISTANCE MODELS (AS A FUNCTION OF ELEVATION OR LAND COVER) AND GENETIC DISTANCE (F_{ST}) ALONE AND AFTER PARTIALLING OUT THE EFFECT OF EUCLIDEAN DISTANCE (IBD). N AND S STAND FOR NORTH AND SOUTH RANGE OF VALLEY OAK. SIGNIFICANT VALUES ARE INDICATED IN BOLD.

Model	Mantel r	P value	Optimized parameter value
$F_{ST} \sim \text{IBD}$	0.16	0.001	
$F_{ST} \sim \text{Elevation}$	0.64	0.001	$E_{opt} = 200 \text{ m (N), } 1100 \text{ m (S), } R_{max} = 25$
$F_{ST} \sim \text{Land cover}$	0.25	0.041	$X=0.25, R_{max}=25$
$F_{ST} \sim \text{Elevation} \mid \text{IBD}$	0.63	0.001	$E_{opt} = 200 \text{ m (N), } 1100 \text{ m (S), } R_{max}=25$
$F_{ST} \sim \text{Land cover} \mid \text{IBD}$	0.23	0.760	$X=0.25, R_{max}=25$

The correlation between elevation resistance and land cover resistance was not significant ($r=0.32$, $P=0.09$). The full model showed that elevation resistance was significant ($P<0.001$) in determining genetic variation, whereas land cover resistance was not ($P=0.76$). In the reduced model with land cover resistance as the only fixed variable, land cover resistance was significant ($P= 0.02$). The reduced model with elevation resistance as the fixed variable was selected as the best model to describe genetic variation (Table III).

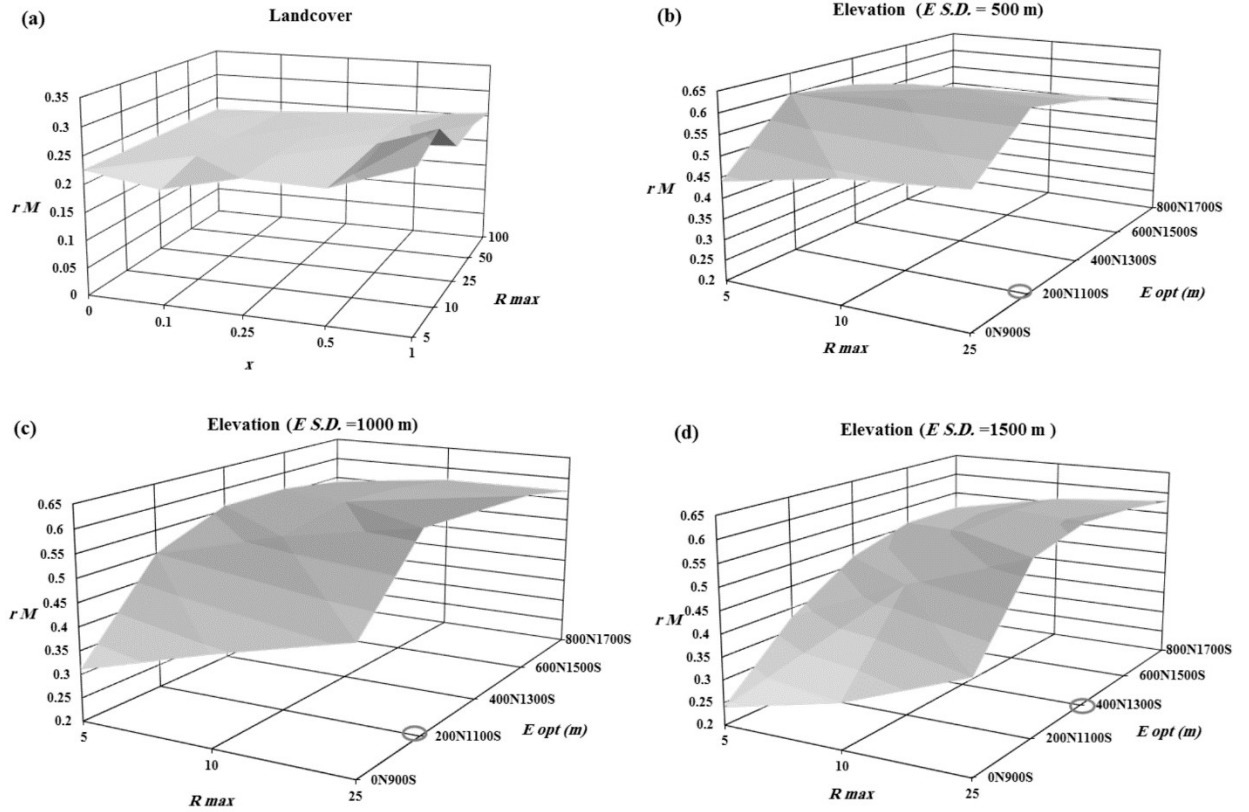


Figure 2. Different scenarios representing Mantel correlation (rM) between genetic distance (F_{ST}) and resistance as a function of Elevation and land cover. R_{max} is the maximum resistance (x- axis) and E_{opt} is optimum elevation (z- axis) in the elevation scenarios. X is the response shape in the land cover scenarios. The resistance model with peak of support for highest correlation to genetic distance is shown with a grey oval.

The Bayesian estimations of migration rates were low for many of the populations (Table IV). Nevertheless, they revealed significant gene flow occurring for the eastern and western populations. Gene flow was asymmetric for most site pairs (Figure 3).

Table III. PARAMETER ESTIMATES FOR THE LINEAR MIXED EFFECTS MODELS. ELEVATION AND LAND COVER RESISTANCE SURFACE ARE THE EXPLANATORY FIXED VARIABLE AND F_{ST} IS THE RESPONSE VARIABLE. EFFECT OF EUCLIDIAN DISTANCE WAS MEASURED IN THE UNIVARIATE MODEL. BETA, STANDARD ERROR, T-VALUE, P VALUE ESTIMATES ARE FROM THE MIXED EFFECT MODEL FIT BY RESTRICTED MAXIMUM LIKELIHOOD USING LME4.

Factor	Parameter	β	S.E.	t value	P value	AIC
Elevation and landcover	Intercept	-0.0050	0.0129	-0.46	0.65	-279.7
	Elevation	0.0019	0.0003	5.56	<0.001	
	Landcover	0.0003	0.0010	0.31	0.76	
Elevation	Intercept	-0.0030	0.0109	-0.35	0.73	-281.6
	Elevation	0.0019	0.0003	6.29	<0.001	
Landcover	Intercept	0.0256	0.0144	1.78	0.08	-256.5
	Landcover	0.0029	0.0011	2.43	0.02	
Euclidian distance	Intercept	0.0472	0.0092	4.75	<0.001	-252.7
	Euclidian distance	0.0002	0.0002	1.36		

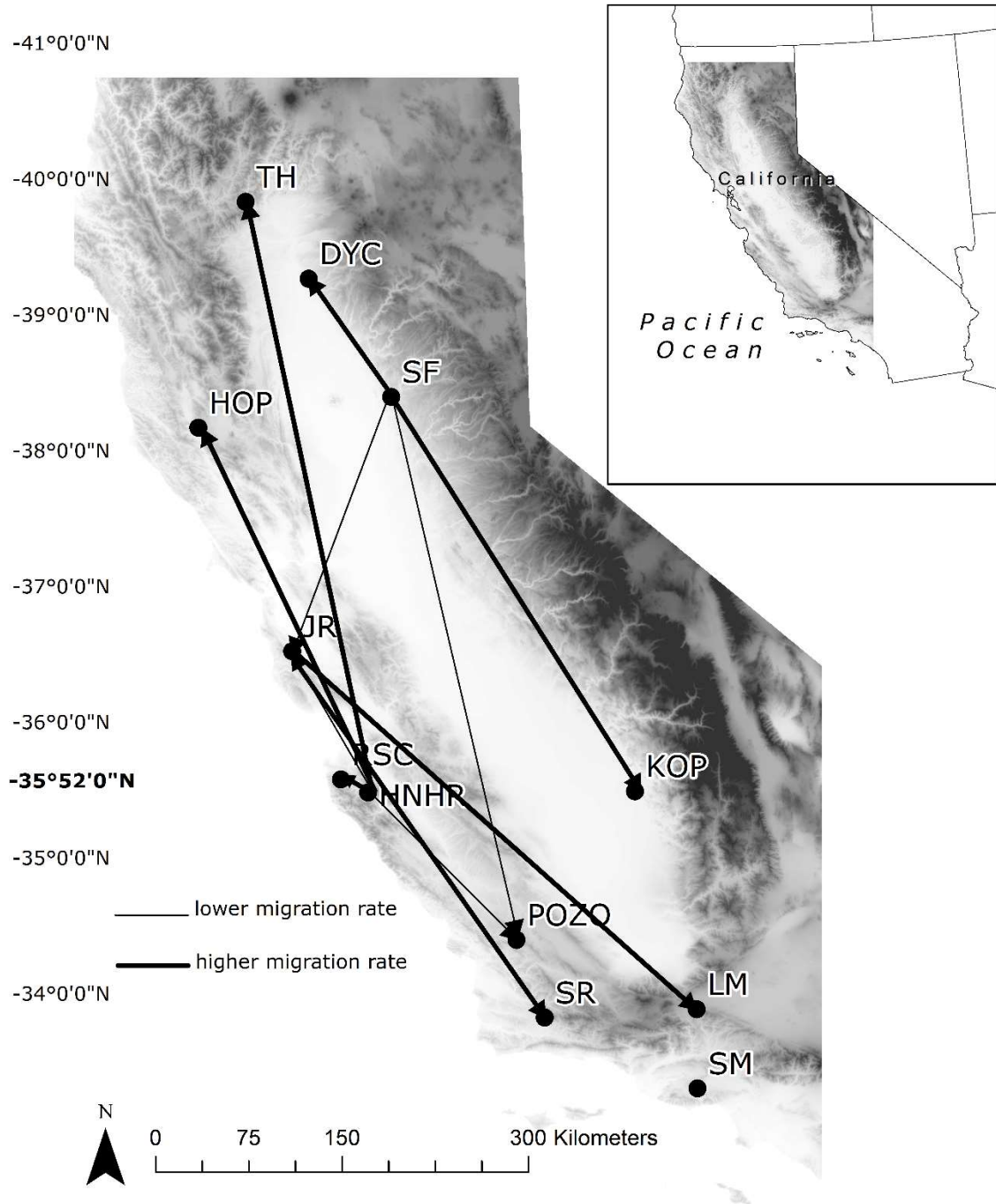


Figure 3. Recent migration pattern for the twelve valley oak sampling sites using BayesAss. The informative (>0.100) values of migration rate is shown. Thicker lines show migration rate >0.2 and thinner lines show migration rate <0.2 . The latitude in which we used to divide valley oak habitat range into north and south is shown in bold.

Table IV. BAYESIAN ESTIMATES OF RECENT MIGRATION RATES IN BAYESASS AMONG 12 VALLEY OAK POPULATIONS. UNDERLINED VALUES ON THE DIAGONAL INDICATE THE PROPORTION OF INDIVIDUALS IN EACH GENERATION THAT ARE NOT MIGRANTS (RESIDENT POPULATIONS). SIMULATIONS SHOW THAT IN INSTANCES WHERE THERE IS NO INFORMATION IN THE DATA, MIGRATION RATE MEAN AND 95% CONFIDENCE INTERVAL FOR DATA SETS WITH 12 POPULATIONS ARE 0.0150 (0.000, 0.100). BOLD VALUES SHOW INFORMATIVE (>0.100) MIGRATION RATES.

From	To											
	TH	DYC	SF	KOP	LM	SM	SR	POZ	HNR	RSC	JR	HOP
TH	<u>0.679</u>	0.004	0.001	0.004	0.005	0.001	0.004	0.004	0.002	0.004	0.003	0.004
DYC	0.003	<u>0.682</u>	0.001	0.004	0.005	0.001	0.004	0.004	0.002	0.004	0.004	0.004
SF	0.010	0.266	<u>0.982</u>	0.265	0.011	0.001	0.030	0.139	0.013	0.004	0.112	0.030
KOP	0.003	0.004	0.001	<u>0.679</u>	0.005	0.001	0.004	0.004	0.002	0.004	0.004	0.004
LM	0.003	0.004	0.001	0.004	<u>0.687</u>	0.001	0.004	0.004	0.002	0.004	0.004	0.004
SM	0.003	0.004	0.001	0.004	0.007	<u>0.987</u>	0.004	0.005	0.003	0.004	0.005	0.004
SR	0.003	0.004	0.001	0.004	0.005	0.001	<u>0.681</u>	0.004	0.002	0.004	0.004	0.004
POZ	0.004	0.004	0.001	0.004	0.006	0.001	0.011	<u>0.706</u>	0.003	0.004	0.004	0.004
HNHR	0.245	0.007	0.002	0.008	0.041	0.001	0.025	0.102	<u>0.955</u>	0.279	0.111	0.251
RSC	0.003	0.004	0.001	0.004	0.005	0.001	0.004	0.004	0.002	<u>0.679</u>	0.004	0.004
JR	0.034	0.006	0.001	0.013	0.210	0.001	0.229	0.015	0.005	0.004	<u>0.699</u>	0.010
HOP	0.003	0.004	0.001	0.004	0.005	0.001	0.004	0.004	0.002	0.004	0.004	<u>0.681</u>

2.5. Discussion

Valley oak demonstrates modest genetic structure across the species' range (Grivet et al. 2007; Ashley et al. 2015). Our results revealed a significant but weak relation between Euclidian distance and genetic distance across valley oak's range. Furthermore, we did not find land cover to be a significant predictor of genetic differentiation among populations. In contrast, elevation

provided an important factor for explaining valley oak genetic structure. This result is in accordance with other studies that have found stable habitat conditions and topographic features to be the most relevant factors determining population differentiation within the California region (Calsbeek et al. 2003; Davis et al. 2008; Lancaster and Kay 2013).

Land cover was not a strong indicator of gene flow. This may be due to the fact that the adult trees that were sampled were in most cases established over 100 years ago, before most of the anthropogenic landscape changes in this region occurred. Our measure of landscape resistance reflects the current landscape, whereas genetic distance reflects historic gene flow. Although land cover changes are likely to eventually have strong population effects through loss of corridors and stepping stones, there is likely to be a considerable time lag in response, especially in long-lived species (Wright 1943; Waples 1998). This mismatch can be an issue when studying landscape genetics in landscapes that are changing rapidly. On the other hand, land cover may offer little resistance to pollen movement, as has been shown in valley oak (Abraham et al. 2011) and other oak species (Ashley 2010, Craft and Ashley 2010).

After dividing the distribution of valley oak latitudinally, we deduced that gene flow was restricted by high elevations in the northern part of its range and by high elevations and the low elevation of Central Valley further south. Our results provide support for the hypothesis put forth by previous studies that topographic features such as mountain ranges and the large, flat Central Valley impact patterns of gene flow in this species (Grivet et al. 2006; Sork et al. 2010; Ashley et al. 2015).

We found a greater resistance effect of elevation in the southern range of valley oak. In other words, the Central Valley is a smaller barrier to gene flow as valley oaks grow at lower

elevation in the more northern part of its range, whereas in the southern part of its range where they inhabit higher elevations, the Central Valley is far below their optimum elevation. This supports the results of Grivet et al. (2007), who found shared chloroplast haplotypes between eastern and western populations north of the Monterey Bay area indicating connectivity in the north part of Central Valley. Similarly, Sork et al. (2010) found that gene flow in valley oak is less restricted in the east–west direction in the northern part of its range, probably due to a strong riparian network in the north. These results all support the conclusion that topographic features have a greater impact on southernmost populations of this species.

Our results indicate that a main landscape feature of the Central Valley that acts as a barrier is its vast low terrain, whereas valley oaks grow and show high productivity potential in mid elevations (Grivet et al. 2007). Diversification and establishment of spatial genetic structure across California’s floristic province coincide with the formation of California’s mountain ranges and aridification in the region (Calsbeek et al. 2003; Lancaster and Key 2013). Topography of an area influences water availability (Sork et al., 2010), species composition and valley oak’s climate niche (Tzedakis et al. 2002).

Our estimates of recent migration rates show higher gene flow north– south than east–west across the Central Valley (Figure 3), as previously reported by Grivet et al. (2008) and Sork et al. (2010). We did, however, detect evidence of some east-west gene flow. We also saw more connections in the west, which is in accordance with Grivet et al. (2007). In the west, JR and HNHR were the most important gene donors while in the east, SF was an important gene donor. These nodes appear to facilitate gene flow by connecting distant populations through a series of migrational routes that mostly occur in the northern Central Valley and should be prioritized for conservation efforts.

The only notable gene flow crossing the southern Central Valley was from SF to POZO, but we suggest that in this case pollen has not directly crossed the Central Valley but rather has occurred through chains of populations, with recent migration between SF and JR (0.112), JR and HNHR (0.111) and HNHR and POZO (0.102). Our results also indicate that gene movement occurs in long distance events and that all populations of valley oak are connected to at least one other population either directly or by a chain of populations. The exception is the Santa Monica population, as previously reported by Ashley et al. (2015). Populations in the Santa Monica mountains in the Transverse ranges compose a distinct group and should be the focus of conservation efforts (Grivet et al. 2008; Ashley et al. 2015).

In California, an increase in temperature associated with climate change could increase vegetation productivity given adequate moisture availability, especially in cooler regions of the state along the north-central coast and at high elevations, and could also promote advancement of grassland and reduction of forest particularly in the southern end of the Central Valley (Leinhan et al. 2003). We therefore predict higher connectivity of northern populations compared to the south because of more contiguous forest and riverine ecosystems. We also predict that the southern end of Central Valley will become a greater barrier in the future. Higher connectivity of northern populations may facilitate resilience to climate change through dispersal of alleles and genotypes better adapted to changing conditions.

Further research into the role and influence of other landscape variables such as slope and aspect will improve our understanding of gene flow for this species. For example, the role of slope and aspect in structuring valley oak populations may be important for steep and opposing north and south slopes such as the transverse ranges if pollen is unable to reach the other side. Future studies would also benefit by including more study sites and marker loci to further

elucidate ecological barriers to gene flow. Using more loci would improve resolution as the magnitude of correlations between landscape pattern and genetic structure of a population of organisms is highly dependent on the number of loci analyzed per individual (Landguth et al., 2012).

The more genetically isolated populations located south of the Transverse Ranges are at great risk of diversity loss and thus likely to be more constrained in their ability to tolerate rapid climate change. Although long distance pollen dispersal is common in oaks (Ashley et al. 2010) and seed dispersal can go beyond local sites (Sezen et al. 2005), the diversity of the pollen/seed pool of the original source is also an important factor for adaptation to climate change. A long-term connectivity plan to restore valley oaks throughout their historical distribution, especially in mid-elevation areas, would be particularly valuable. Conservation strategies should include restoring and conserving suitable habitat for valley oak based on optimum elevation and topographic structure to maintain functional connectivity across its habitat range, protecting the nodes of its gene flow network, maintenance of valley oak habitat especially in the northern Central Valley, and protection of riverine ecosystems that create migrational corridors and enhance gene flow.

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CHAPTER THREE

3. MANAGEMENT SLOWS DOWN INVASION BY NON-NATIVE PLANTS BUT DOES NOT PREVENT COMMUNITY CHANGE OVER 35 YEARS IN URBAN FORESTS OF THE MIDWESTERN USA

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Gharehaghaji, M., Kobal, S., Reklau, R. and Minor, E.S., 2019. Management slows down invasion by non-native plants but does not prevent community change over 35 years in urban forests of the Midwestern USA. *Forest Ecology and Management*, 448, pp.424-431. Forest Ecology and Management, 448, pp.424-431).

3.1. Abstract

Urban forests are threatened by land cover change and invasive species but little is known about how they are changing over time. Furthermore, although management is sometimes used to maintain native communities, we have little information about the long-term outcomes of forest management actions. In this study, we examined current status and long-term changes in 35 urban forest plots in DuPage County, Illinois (USA). From 1979 to 2014, in five-year intervals, presence/absence of all woody species was recorded in the plots. Environmental conditions in and surrounding the plots were measured in the field or with GIS. With these data, we analyzed trends and changes in the community, looked for evidence of biotic homogenization, and examined drivers of non-native species. We found a significant change in community composition over time but no evidence of biotic homogenization in either managed or unmanaged plots. There was a significant increase in non-native species richness over time but

no change in richness of other species groups. Vegetation management such as fire prescription and clearing seemed to somewhat decrease the number of non-native species, but did not increase the number of more desirable species. Distance to agriculture and deer control frequency determined the variation in both non-native species abundance and richness. Overall, we conclude that the management activities were able to slow down the spread of some undesirable species but did not prevent their increase over time. More consistent management, as well as collaboration with stakeholders outside the forest preserves, is likely needed to maintain native communities.

3.2. Introduction

Understanding variation in plant community composition across space and time is a central goal of vegetation ecology (Anderson et al., 2011). This topic is particularly crucial in urban forests due to the worldwide trend toward urbanization and threats to urban green spaces (McPherson, 1997). Urban forests include street trees, trees in city parks, green belts, and forest patches inside or around urban areas (Moeller, 1977). These forests provide a variety of critical ecosystem services, harbor a high diversity of species, and play an important recreational, spiritual, and cultural role in the lives of city residents (Bolund and Hunhammar, 1999). Evaluating long-term dynamics of urban forests will help determine whether forests are resilient to disturbances and inform choices between competing demands of anthropogenic use versus conservation of biodiversity.

Many factors contribute to changes in urban forest structure and composition. These include direct human modification of the forest and ‘natural’ factors such as disturbances, herbivore populations, and climate change (Keles et al., 2017). The latter set of factors can be the

direct or indirect result of human activity as well. For example, forest fires are often directly suppressed due to safety concerns, leading to dense-canopied forests dominated by shade-tolerant species (Nowacki and Abrams, 2008). Indirectly, fire regimes can be altered as a result of non-native species spread (Flory et al., 2015). Another indirect impact of humans can be seen in the increased deer populations resulting from intentional predator elimination in most ecosystems (Terborgh and Estes, 2010), including the north-central and eastern temperate forests of the United States (Hobbs, 1996; Russell et al., 2001). Dense deer populations have profound effects on forest regeneration and composition (Tilghman et al., 1989) and pose significant challenges to the conservation of native plant communities (Griggs et al., 2006) by facilitating the abundance and spread of non-native invasive species (Shen et al., 2016).

Urbanization and other land conversion can also drive forest change. Many native canopy species are sensitive to impacts associated with urbanization (e.g., fragmentation, competition with non-native plants, hydrological changes; Didham et al., 2007) and agricultural land use (e.g., high N deposition due to fertilizer use and fossil fuel combustion; Frey et al., 2004). Land use changes may lead to loss of native species (Czech et al., 2000) and invasion by non-native species (Pennington et al., 2010).

The loss of native species and increase in non-native species can lead to biotic homogenization—the increase in compositional similarity among formerly distinct communities that reduces the ecological uniqueness of local ecosystems (Blair, 2001). Because homogenization often replaces a number of local species with a smaller number of non-native and widespread (ruderal) species, it reduces spatial diversity (McKinney and Lockwood, 1999). Although many of these non-native species thrive in disturbed environments (e.g. urban forests), some also invade, and thus homogenize, relatively undisturbed natural areas (Williamson, 1996).

Homogenization has been documented in forests over the entire northern USA Great Lakes region (Schulte et al., 2007) and in other parts of the world (Naff and Wulf, 2010; Keith et al., 2009). In temperate forests of the Midwestern USA, some important drivers of homogenization include fire suppression (Hanberry et al., 2012), deer overpopulation (Rooney et al., 2004), and invasion by non-native plants (McKinney and Lockwood, 1999). Fire suppression can lead to mesophication, which in turn can lead to biological homogenization (Hanberry et al., 2012). Mesophication of broadleaf forests throughout the eastern United States is occurring via replacement of fire-stabilized oaks and pine by fire-sensitive species, specifically shade-tolerant mesophytic species (Nowacki and Abrams, 2008). Management techniques may be able to counteract homogenization of forests but little research has directly addressed their effectiveness in doing such.

Forest management is often used to impede loss of native species, invasion by non-native species, and biotic homogenization. Restoration-focused management regimes include prescribed fire (Bowles et al., 1994), understory thinning, and non-native shrub removal or clearing (Lorimar et al., 1994). However, vegetation responses to management can vary widely, depending on both the nature of the management and initial stand condition (McRae et al., 2001). Long-term effects of management on forest structure and composition are largely unknown (Arthur et al., 2015) or can be counter-intuitive. For example, some research shows that even with multiple fires, changes in stand structure are often too minor to significantly alter the course of succession (Hutchinson et al., 2012). Other studies show that, even within fire-tolerant vegetation, fire can promote non-native species (D'Antonio and Meyerson, 2002) if it is intense enough to reveal bare mineral soil and open previously closed canopies (Symstad et al., 2014). On the other hand, deer management may be more effective than fire, as studies show that non-

native vegetation cover, abundance, growth, and population growth rates decline when deer are controlled or eliminated (Dávalos et al., 2015; Nuzzo et al., 2017).

Most studies to-date have explored the role of individual factors such as urbanization (Pennington et al., 2010), management (McGarvey et al., 2013) or local environmental conditions (Oliveira-Filho et al., 2001) on forest communities. Furthermore, most ecological studies are limited to a relatively short time period, often just a few years (Hutchinson et al., 2012). However, managers need information about the impact of all of these factors over longer time periods to make informed decisions about the future of urban forests. This research attempts to fill that gap in knowledge by examining changes in community composition over a 35-year period (1979-2014) in forests in DuPage County, Illinois. Using data from 35 forest plots in an urbanizing landscape, we explore community change, homogenization, and changes in individual species and groups of species (e.g. non-native, ruderal, and shade-tolerant species, which all contribute to biotic homogenization in our study area). Specifically, we ask the following questions:

1. Has the woody plant community in DuPage County Forest Preserves changed over 35 years?
Have the communities become more homogenized?
2. What are the trends and patterns in individual species occurrence over time? How have particular woody species or groups of woody species, such as native and non-native species, shade tolerant and intolerant species, and habitat specialists, changed over time?
3. What are the most important drivers of invasion by non-native species?
4. What is the role of management in the changing forest? Is management effective in controlling the non-native species and maintaining the conservation value of plots? Could management techniques prevent biotic homogenization?

Our work contributes unique insight into long-term forest management and plant invasions in an urban landscape.

3.3. Methods

3.3.1. Study area

This study makes use of a dataset collected over a 35-year period in DuPage County in northern Illinois (USA) (Figure 4). DuPage County is one of the “collar” counties of the Chicago metropolitan area. It has a population of 916,924 residents according to the 2010 decadal census and is the second most populated county in Illinois; its population is expected to grow in the future because of its proximity to Chicago (DuPage County Statistical Profile, 2011). The study region has a humid continental climate with mean temperatures of 23°C in July and -10°C in January, and mean annual precipitation of 92 cm (based on climate normals from Illinois State Climatology). Soil is mostly very deep and moderately well drained or well drained (Kelsey 2000).

Prior to European habitation, about 85% of DuPage County was tallgrass prairie and the remaining 15% was oak-maple forest (Thompson, 1985). The vegetation of this region was historically controlled by an interaction between landscape fire breaks and fire processes related largely to Native American activity (McBride and Bowles, 2001). However, with the cessation of annual fires at the time of European settlement, these open communities began to fill in rapidly and develop closed-canopy forests (Fahey et al., 2012). The county manages many of these forests in their Forest Preserve District.

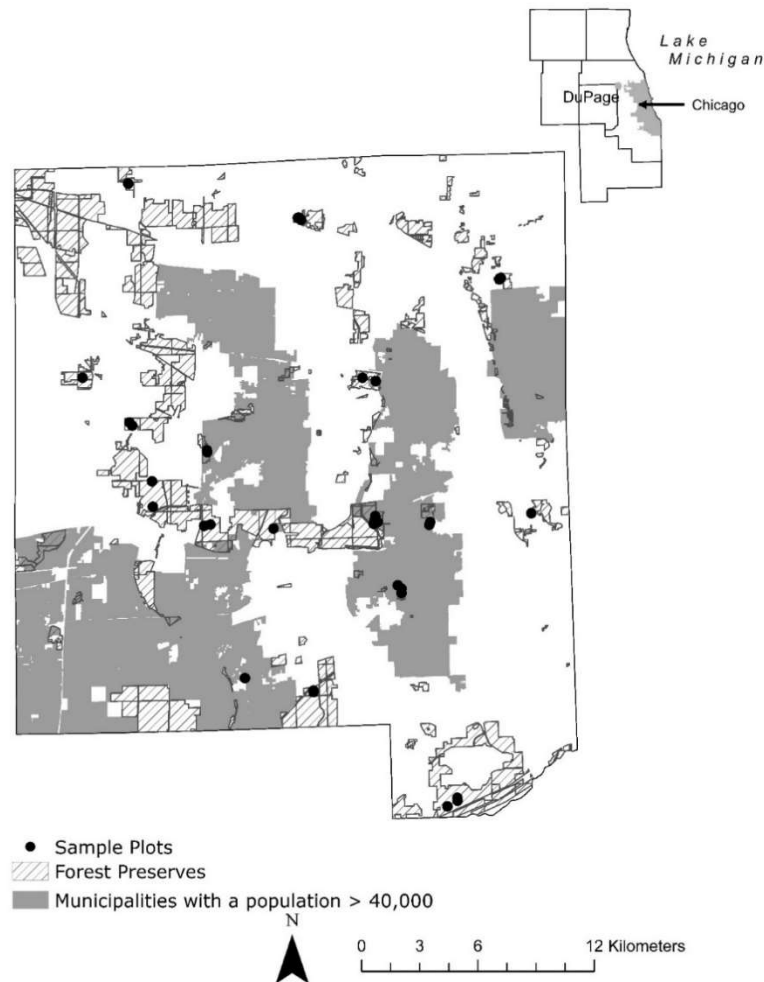


Figure 4. Distribution of forest preserves, populated municipalities (> 40,000 people), and our sample locations in DuPage County, Illinois, USA. Population data from <http://dupage.maps.arcgis.com>

In total, 17 forest preserves around the county were selected for long-term monitoring. Thirty-five sample plots were placed inside those preserves to represent typical woodlands in the county. The plots were mostly comprised of white oak (*Quercus alba*), red oak (*Q. rubra*), bur oak (*Q. macrocarpa*), wild black cherry (*Prunus serotina*), white ash (*Fraxinus americana*),

American elm (*Ulmus americana*), sugar maple (*Acer sacharum*), and basswood (*Tilia americana*). Each plot is 47,000 square feet (approximately 0.45 Ha).

No management occurred in the plots before the monitoring period began. In subsequent years, vegetation management occurred in 26 of the 35 plots. Vegetation management usually comprised prescribed fire and/or understory clearing, but sometimes included herbicide as well. Fire was usually applied between November until early December, or between late March and mid-April before green-up. Fires were managed to advance slowly against the wind in a controlled fashion. Clearing focused on preserving desirable trees in the understory by removing or killing other plants that threatened their survival or development. This generally included removal of non-native trees and shrubs and thinning of abundant native tree species through cutting and herbicide application.

In addition to vegetation management at the plot level, deer management was applied at regular intervals (often annually) across 11 forest preserves that included 25 of the plots. Deer management was lethal removal with the goal of reducing the deer population to 6-8 individuals per square kilometer before fawning. Vegetation and deer management decisions are based on the forest preserve district's priorities, logistical constraints, and are intended to maximize the "return on investment" for the district.

3.3.2. Data collection

For the purpose of this study, we focus on change in woody vegetation (including mature trees, small trees, and shrubs) between two time periods: 1979 and 2014. The sample sites were monitored every 5 years (or more frequently) during this time period by scientists and staff of the Forest Preserve District of DuPage County. At each time interval, investigators measured all

mature trees (diameter at breast height > 3.5 inches [9 cm]) in each plot. To survey small trees and shrubs, 5 (4 m * 4 m) quadrates were randomly placed in each plot. Presence/absence of all woody species (trees and shrubs) was recorded since 1979, and abundance of mature trees was recorded over the same time period, but abundance of small trees and shrubs was only measured starting in 2002.

Each woody species was classified according to several aspects of its biology. Plant species native to the Chicago Region were identified according to Swink and Wilhelm (1994). Native species were classified as specialists or ruderals based on their coefficient of conservatism. This coefficient, ranging from 0 – 10, indicates a species' tolerance to disturbance and fidelity to habitat integrity (Taft et al., 1997). Native species with coefficients < 4 are considered ruderal species that can establish in disturbed habitats, while those with coefficients of 4 or greater specialize on 'unaltered landscapes' and are found in more intact native habitats. Non-native species were not assigned a numerical value. Species were also classified according to their shade tolerance. Shade tolerance / intolerance was determined using Niinemets and Valladares (2006) classification and some online resources including the Lady Bird Johnson Wildflower center (wildflower.org), the University of Minnesota extension office (extension.umn.edu) and the Missouri Botanical Garden (missouribotanicalgarden.org), as there was no single resource that included all species in the study area. All native and non-native species that were described to tolerate shade, partial shade, or 'full sun to full shade' were classified as shade tolerant. Species that could tolerate full sun only were classified as shade intolerant. All species, and their classifications, are listed in Table X, Appendix A.

We gathered a set of variables that described the environment at each plot, most of which were only measured once during the 35-year period. At each random quadrat, the amount of light

was determined using a standard photographer's light meter. Readings were taken in 2014 on cloudless summer days between 10 a.m. and 2 p.m. and expressed as a percentage of the available light. Slope and aspect of the plot were measured using Illinois Statewide 30-Meter Digital Elevation Model (<http://www.isgs.illinois.edu>). Clay and organic matter in the soil were calculated using Soil Survey Geographic database (SSURGO). Initial (1979) native woody species richness was measured to test if more diverse native communities are less invasible (i.e., biotic resistance potential). Pre-settlement vegetation was defined as 'forest' or 'non-forest' using the map created by Bowles et al. (1998). Vegetation management was described in terms of number of unique events (e.g., number of fires) but also in binary terms (managed or not managed). Deer management was described as the number of deer control events in a plot throughout 35 years. Finally, we measured a number of larger-scale variables around each plot using ArcGIS 9.3 (ESRI 2016). These include percent tree canopy cover in a 500 m radius, distance from the plot to the edge of the forest, distance to the closest paved road or trail, distance to the closest residential area, distance to a river, and distance to agriculture. All variables and their sources are listed in Table XI, Appendix B.

3.3.3. Data Analysis

3.3.3.1. Community-level analyses

To examine change in the entire forest community between 1979 and 2014, we used permutational multivariate analysis of variance (i.e., PERMANOVA) and looked for an effect of year, plot, and vegetation management on community composition. Because abundance of small trees and shrubs was not measured until 2002, we used presence/absence data to describe the community in the two years, and Sorensen distance to measure pairwise compositional

dissimilarity between sites and years. The test was conducted in the “vegan” package in R (Oksanen et al., 2017) with 999 permutations.

Changes in community composition were visualized by performing non-metric multidimensional scaling (NMDS) on the Sorensen distances. This can illustrate shifts in the communities, direction of compositional change, and changes in dispersion. The axes of an NMDS graph do not indicate specific ecological variables, but are created to best represent the similarities and differences between plots. We plotted the vegetation in both years for all plots combined, as well as managed and unmanaged plots separately. Successional vectors were added to visualize the pairwise trend between plots from 1979 to 2014 (Figure 10, Appendix C). NMDS was performed in PC-ORD (McCune and Mefford, 2011) in two dimensions and with a maximum of 250 random starts to achieve convergence.

To test for biotic homogenization in the study sites, we used a distance-based test for homogeneity of multivariate dispersions (PERMDISP; Anderson et al., 2008), comparing dispersion of communities in 1979 to dispersion of communities in 2014. A smaller dispersion in 2014 would indicate reduced beta diversity and biotic homogenization. Managed and unmanaged plots were examined separately. We applied the function “betadisper” in package “vegan” in R, which is a multivariate analogue of Levene's test for homogeneity of variances. Differences among sample locations in each time period were calculated with the Sorenson index. To test the null hypothesis that beta diversity does not differ between the two years for managed and unmanaged plots, we calculated an F-statistic to compare the average distance of each sample to the centroid of the group. We calculated a P-value from 999 permutations of least-squares residuals.

3.3.3.2. Analyses of species groups

To examine changes in particular groups of woody species between 1979 and 2014 within managed and unmanaged plots, we tested six nested generalized linear mixed models (GLMMs) in the package “lme4” (Bates et al., 2015) in R. For this analysis, “management” refers to plot-level vegetation management such as prescribed fire and clearing. First, we examined changes in number of native and non-native species in each plot. Next, we looked more closely at the native species by examining changes in ruderal and specialist species (i.e., species with a coefficient of conservatism < 4 or ≥ 4 , respectively). Finally, we examined if the number of shade-tolerant and intolerant species changed within 35 years. We applied the Poisson distribution for native, specialist, generalist, shade-tolerant, and shade-intolerant species, and we applied the negative binomial distribution for non-native species. Because several sample plots were contained in the same forest preserve, we specified plot as a random effect nested in forest preserves, while year and management were fixed effects.

To further understand invasion by non-native species, we used hierarchical linear models in the form of nested generalized linear mixed models (GLMMs) to identify potential drivers of richness and abundance of non-native species in 2014 (the most recent year that data were collected). Potential drivers included the variables we measured for each plot (i.e., the local environment, management activities, and landscape-scale factors listed in Table XI, Appendix B). Distance to river was excluded because most plots were more than 100 m away from river. We used the negative binomial distribution to model non-native species abundance and the Poisson family to model non-native species richness. As before, plot was a random effect nested in forest preserve. Model selection was based on a stepwise “backward” method that started with the full model (i.e., included all possible predictor variables). We removed the least significant

explanatory variable first and continued removing non-significant variables ($p > 0.05$) one at a time until the model contained nothing but significant variables.

3.3.3.3. Analyses of individual species

To explore trends in occurrence of individual woody species over time, we used nested GLMMs with binomial distribution for each species found in the plots. We used the matrix of presence and absence of each species in 35 plots over 35 years as the response variable, and set time as the explanatory variable. Time was in five-year intervals from 1979 to 2014. Plot was a random factor nested in forest preserve. We identified species that showed significant increases or decreases in their distribution over time. We also predicted the number of occurrences for each species in year 2029 (representing a 50-year time period) using each species' model slope, intercept and the function "plogis" in R.

3.4. Results

3.4.1. Community-level analyses

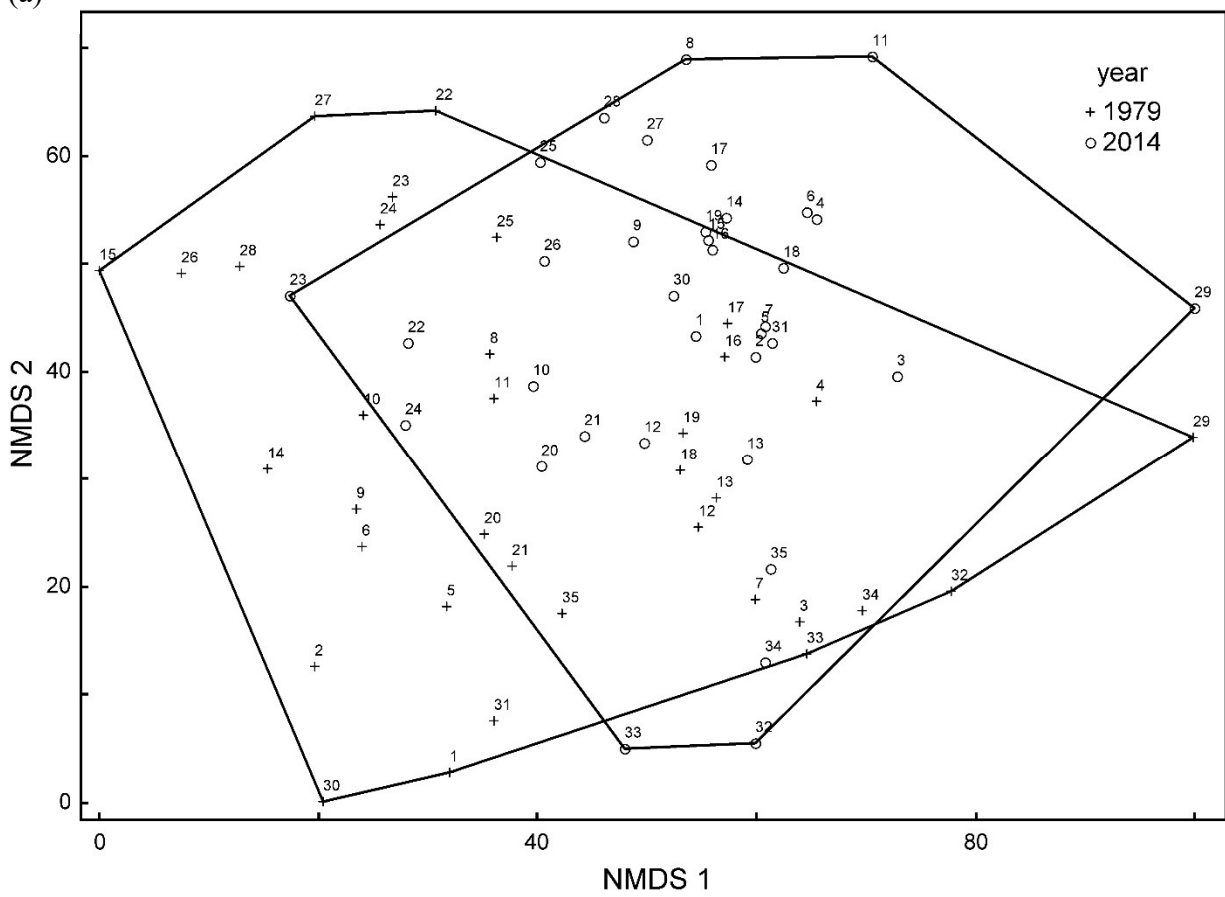
Over the 35-year sampling period, we found 57 tree species in the plots. Forty-three tree species were native and 14 were non-native. Over the same period, 43 species of shrubs were identified in the plots, including 26 native and 17 non-native species. According to the PERMANOVA, the forest community changed significantly between 1979 and 2014 ($F=9.08$, $P=0.001$). Plot, time and vegetation management explained 61%, 11% and 8% of variation in the woody species community, respectively (Table V). The NMDS showed a slight shift of the community in the managed plots and a larger shift in the unmanaged plots (Figure 5; Figure 10,

Appendix C). The PERMDISP test for managed plots ($F=1.821$, $P= 0.2$) and unmanaged plots ($F=0.561$, $P= 0.461$) did not show any sign of homogenization in either set of communities.

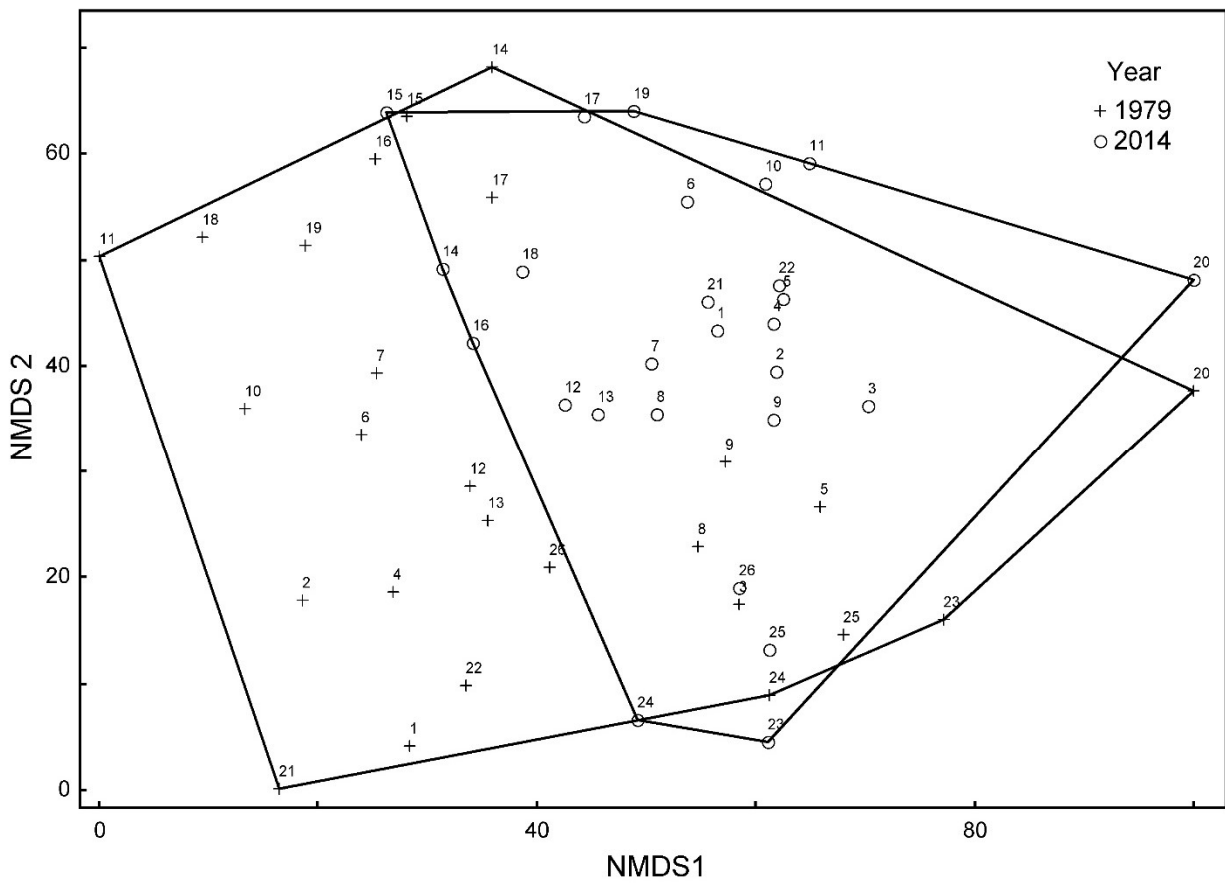
Table V. RESULTS FROM THE MULTIVARIATE PERMUTATIONAL ANALYSIS (PERMANOVA) OF DIFFERENCES IN WOODY PLANT COMMUNITIES BASED ON PLOT (N = 35), YEAR (1979 VS. 2014), AND VEGETATION MANAGEMENT (MANAGED VS. UNMANAGED)

PERMANOVA	df	SS	MS	F	R ²	P
Plot	34	3.716	0.109	2.962	0.613	0.001
Year	1	0.679	0.679	18.403	0.112	0.001
Management	3	0.519	0.173	4.689	0.085	0.001
Residuals	31	1.143	0.036		0.188	
Total	69	6.058			1	

(a)



(b)



(c)

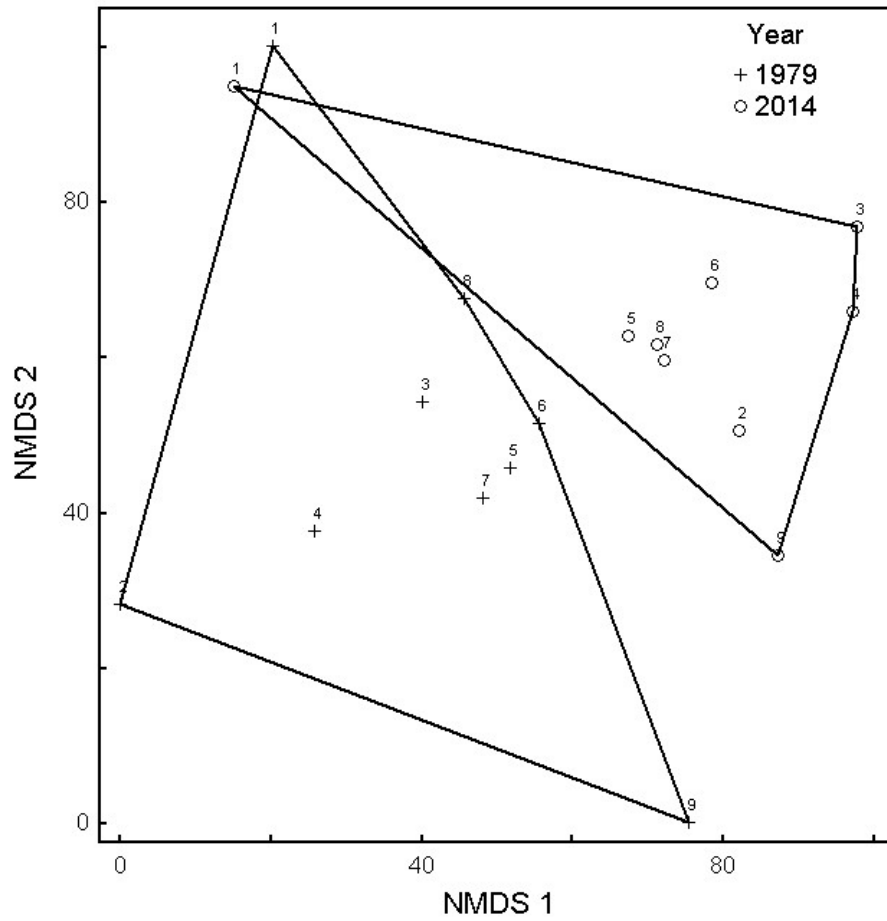


Figure 5. Non-metric multidimensional scaling (NMDS) of woody species community composition in a) all plots combined, b) managed plots, and c) unmanaged plots in year 1979 and 2014. Plots are numbered (with consecutive numbers from 1 to 35 for all plots, 1 to 26 for managed plots, and 1 to 9 for unmanaged plots) to facilitate comparisons between years. Successional vectors are shown in Figure 10, Appendix C.

3.4.2. Analyses of species groups

The only group of woody species that showed a significant change in richness over time or with management were non-native species, which increased over time and decreased with management (Table VI). There was not a significant interaction between time and management in any of the models.

Table VI. NESTED GENERALIZED LINEAR MIXED EFFECTS MODELS FOR PARTICULAR GROUPS OF WOODY SPECIES (NATIVE, NON-NATIVE, SPECIALIST, RUDERAL, SHADE-TOLERANT, SHADE-INTOLERANT SPECIES) AND HOW THEY HAVE CHANGED OVER TIME (1979-2014) AND WITH VEGETATION MANAGEMENT. SAMPLE PLOTS ARE A RANDOM VARIABLE NESTED WITHIN FOREST PRESERVES. SIGNIFICANT VARIABLES (AT $P \leq 0.05$) ARE SHOWN IN BOLD TEXT. NON-SIGNIFICANT VARIABLES THAT SHOW A TREND ($P \leq 0.1$) ARE SHOWN IN ITALICS.

Response variable	Explanatory variable	<i>B</i>	S.E.	Z-value	P value
Native species richness	Intercept	3.067	0.048	68.001	< 0.001
	Time	-0.059	0.060	-0.975	0.330
	Management	0.018	0.099	-0.189	0.850
	Time*Management	-0.132	0.121	-1.094	0.274
Non-native Species richness	Intercept	0.649	0.171	3.790	< 0.001
	Time	1.049	0.209	5.005	< 0.001
	Management	-0.894	0.290	3.079	0.002
	Time*Management	-0.436	0.352	-1.239	0.215
Specialist Species richness	Intercept	2.568	0.063	40.685	< 0.001
	<i>Time</i>	<i>-0.138</i>	<i>0.079</i>	<i>-1.745</i>	<i>0.081</i>
	Management	0.145	0.129	-1.121	0.262
	Time*Management	-0.103	0.165	-0.623	0.533
Ruderal Species richness	Intercept	2.112	0.068	30.976	< 0.001
	Time	0.058	0.095	0.618	0.536
	<i>Management</i>	<i>-0.222</i>	<i>0.124</i>	<i>1.795</i>	<i>0.072</i>
	Time*Management	-0.196	0.179	-1.098	0.272
Shade-tolerant species richness	Intercept	3.099	0.047	65.861	< 0.001
	<i>Time</i>	<i>0.099</i>	<i>0.057</i>	<i>1.729</i>	<i>0.083</i>
	Management	-0.110	0.093	1.183	0.236
	Time*Management	-0.112	0.109	-1.033	0.301
Shade-intolerant species richness	Intercept	0.479	0.181	2.646	0.008
	Time	-0.295	0.231	-1.274	0.202
	Management	<i>0.725</i>	<i>0.431</i>	<i>-1.682</i>	<i>0.092</i>
	Time*Management	0.518	0.525	0.987	0.323

The selected model for abundance of non-native species showed that distance to agriculture, deer control, light, distance to road, and native richness were important in explaining non-native abundance (Table VII). Non-native species abundance was lower in plots that were farther from agriculture and roads and had more deer control, while it was higher in plots with more native species richness and light. The selected model for richness of non-native species showed that deer control and distance to agriculture both had negative effects on non-native richness (Table VII).

Table VII. NESTED GENERALIZED LINEAR MIXED MODELS FOR NON-NATIVE SPECIES ABUNDANCE AND RICHNESS FOR 35 FOREST PLOTS IN DUPAGE COUNTY, ILLINOIS IN 2014. FINAL MODEL WAS IDENTIFIED USING A BACKWARD STEPWISE APPROACH; SIGNIFICANT ($P \leq 0.05$) VARIABLES ARE SHOWN IN ALPHABETICAL ORDER. COEFFICIENTS ARE STANDARDIZED.

Response variable	Explanatory variable	<i>B</i>	S.E.	Z-value	P value
Non-native species abundance	Intercept	2.994	1.760	1.701	0.088
	Distance to Agriculture	-1.036	0.312	-3.312	<0.001
	Deer control	-0.045	0.014	-3.118	0.002
	Light	0.036	0.013	2.704	0.007
	Native richness	0.072	0.036	1.947	0.050
	Distance to Road	-0.813	0.408	-1.992	0.046
Non-native species richness	Intercept	3.560	0.487	7.312	<0.001
	Distance to Agriculture	-0.477	0.152	-3.130	0.002
	Deer control	-0.029	0.008	-3.414	<0.001

3.4.3. Analysis of individual species

The GLMMs for individual species showed that nine species experienced significant declines and nine species experienced significant expansions throughout 35 years (Table VIII). All species that declined were native, while two thirds of the species that increased were non-native and the rest were native but ruderal.

Table VIII. WOODY SPECIES THAT HAVE DECLINED OR EXPANDED SIGNIFICANTLY IN THE NUMBER OF PLOTS IN WHICH THEY OCCURRED BETWEEN 1979 AND 2014, ALONG WITH A PREDICTION OF NUMBER OF PLOTS IN WHICH THEY WILL OCCUR IN THE FUTURE (2029). RESULTS ARE BASED ON NESTED GENERALIZED LINEAR MIXED MODELS, WITH SAMPLE PLOTS NESTED WITHIN FOREST PRESERVES. * INDICATES NONNATIVE SPECIES.

						Number of plots occupied		
Species	Explanatory variable	<i>B</i>	S.E.	Z-value	P value	1979	2014	2029 (predicted)
Declining species								
Black maple (<i>Acer saccharum ssp. Nigrum</i>)	Intercept	-1.522	0.689	-2.207	0.027	10	3	0
	Time	-0.065	0.019	-3.329	<0.001			
Dotted Hawthorn (<i>Crataegus punctata</i>)	Intercept	-0.860	0.639	-1.345	0.178	12	5	2
	Time	-0.052	0.017	-2.990	0.002			
Downy Arrow wood (<i>Viburnum rafinesquianum</i>)	Intercept	1.483	0.716	2.070	0.038	21	2	0
	Time	-0.203	0.033	-6.151	<0.001			
Frosted Hawthorn (<i>Crataegus pruinosa</i>)	Intercept	-1.907	0.627	-3.039	0.002	4	0	0
	Time	-0.145	0.048	-3.020	0.002			
Iowa crab (<i>Malus ioensis</i>)	Intercept	-0.670	0.64	-1.034	0.301	12	4	0
	Time	-0.091	0.020	-4.400	<0.001			
Hill oak (<i>Quercus ellipsoidalis</i>)	Intercept	-8.372	2.056	-4.071	<0.001	12	3	0
	Time	-0.362	0.113	-3.192	0.001			
Silver Maple (<i>Acer saccharinum</i>)	Intercept	0.072	0.704	0.102	0.918	18	3	0
	Time	-0.147	0.025	-5.731	<0.001			

Table VIII (continued) WOODY SPECIES THAT HAVE DECLINED OR EXPANDED SIGNIFICANTLY IN THE NUMBER OF PLOTS IN WHICH THEY OCCURRED BETWEEN 1979 AND 2014, ALONG WITH A PREDICTION OF NUMBER OF PLOTS IN WHICH THEY WILL OCCUR IN THE FUTURE (2029). RESULTS ARE BASED ON NESTED GENERALIZED LINEAR MIXED MODELS, WITH SAMPLE PLOTS NESTED WITHIN FOREST PRESERVES. * INDICATES NONNATIVE SPECIES.

						Number of plots occupied		
Species	Explanatory variable	<i>B</i>	S.E.	Z-value	P value	1979	2014	2029 (predicted)
Declining species (continued)								
Wahoo (<i>Euonymus atropurpureus</i>)	Intercept	-3.081	1.441	-2.138	0.032	7	3	0
	Time	-0.093	0.029	-3.176	0.001			
Wild black currant (<i>Ribes americanum</i>)	Intercept	-1.006	0.596	-1.689	0.091	13	6	3
	Time	-0.051	0.018	-2.774	0.005			
Expanding species								
Amur honeysuckle* (<i>Lonicera maackii</i>)	Intercept	-2.727	1.122	-2.431	0.015	10	29	35
	Time	0.217	0.040	5.319	<0.001			
Burning bush* (<i>Euonymus alatus</i>)	Intercept	-3.557	0.860	-4.136	<0.001	1	11	16
	Time	0.068	0.021	3.265	0.001			
Common blackberry (<i>Rubus allegheniensis</i>)	Intercept	-0.498	0.358	-1.391	0.164	12	24	33
	Time	0.072	0.015	4.709	<0.001			
Common buckthorn* (<i>Rhamnus cathartica</i>)	Intercept	0.733	0.361	2.025	0.042	16	29	34
	Time	0.064	0.017	3.729	<0.001			
Hackberry (<i>Celtis occidentalis</i>)	Intercept	-2.903	0.907	-3.199	0.001	10	26	34
	Time	0.127	0.025	5.090	<0.001			
Honey locust (<i>Gleditsia triacanthos</i>)	Intercept	-4.754	0.860	-5.523	<0.001	1	9	18
	Time	0.096	0.026	3.581	<0.001			
Japanese crab* (<i>Malus sieboldii</i>)	Intercept	-10.079	2.558	-3.939	<0.001	0	12	35
	Time	0.231	0.057	4.023	<0.001			
Multiflora rose* (<i>Rosa multiflora</i>)	Intercept	0.129	0.400	0.322	0.747	15	29	34
	Time	0.079	0.017	4.599	<0.001			
Smooth arrow wood* (<i>Viburnum recognitum</i>)	Intercept	-2.282	0.576	-3.956	<0.001	0	14	30
	Time	0.081	0.017	4.755	<0.001			

3.5. Discussion

We examined plant community changes over a 35-year period in urbanizing woodlands. Our results indicate a clear shift in the woody species community but no evidence of biotic homogenization. Furthermore, we found a general trend towards more non-native species over time. Management of vegetation seemed to somewhat decrease the number of non-native species but did not increase the number of more desirable species. Our analyses provide quantitative information that will allow land managers to better predict how forest communities will respond to management and urbanization.

In general, we found a significant change in species composition over time. There was a clear increase in number of non-native species. Although we found no significant change in native, ruderal, or shade-intolerant species richness over the same period, there was a trend toward fewer specialist species and more shade-tolerant species over time (Figure 6, Table VI) that merits attention and should be considered for appropriate management actions in the future. Some individual species showed a significant change in their distribution. For instance, honey locust (*Gleditsia triacanthos*), a ruderal, shade-intolerant, native species was rare in 1979 but has increased significantly since then. In contrast, the native black maple (*Acer saccharum subsp. nigrum*) and silver maple (*A. saccharinum*) have declined over that time. Furthermore, wahoo (*Euonymus atropurpureus*) and wild black currant (*Ribes americanum*), which are specialist shrubs with high conservation value in DuPage County, dramatically decreased over time. By 2029, we predict that some species such as wahoo and wild black currant will be lost from the community, while others such as Japanese crab (*Malus sieboldii*) will be established. This calls for action toward targeted non-native species along with protecting both highly specialized

native species and also some native species with a medium coefficient of conservatism that will promote native diversity in forest habitats.

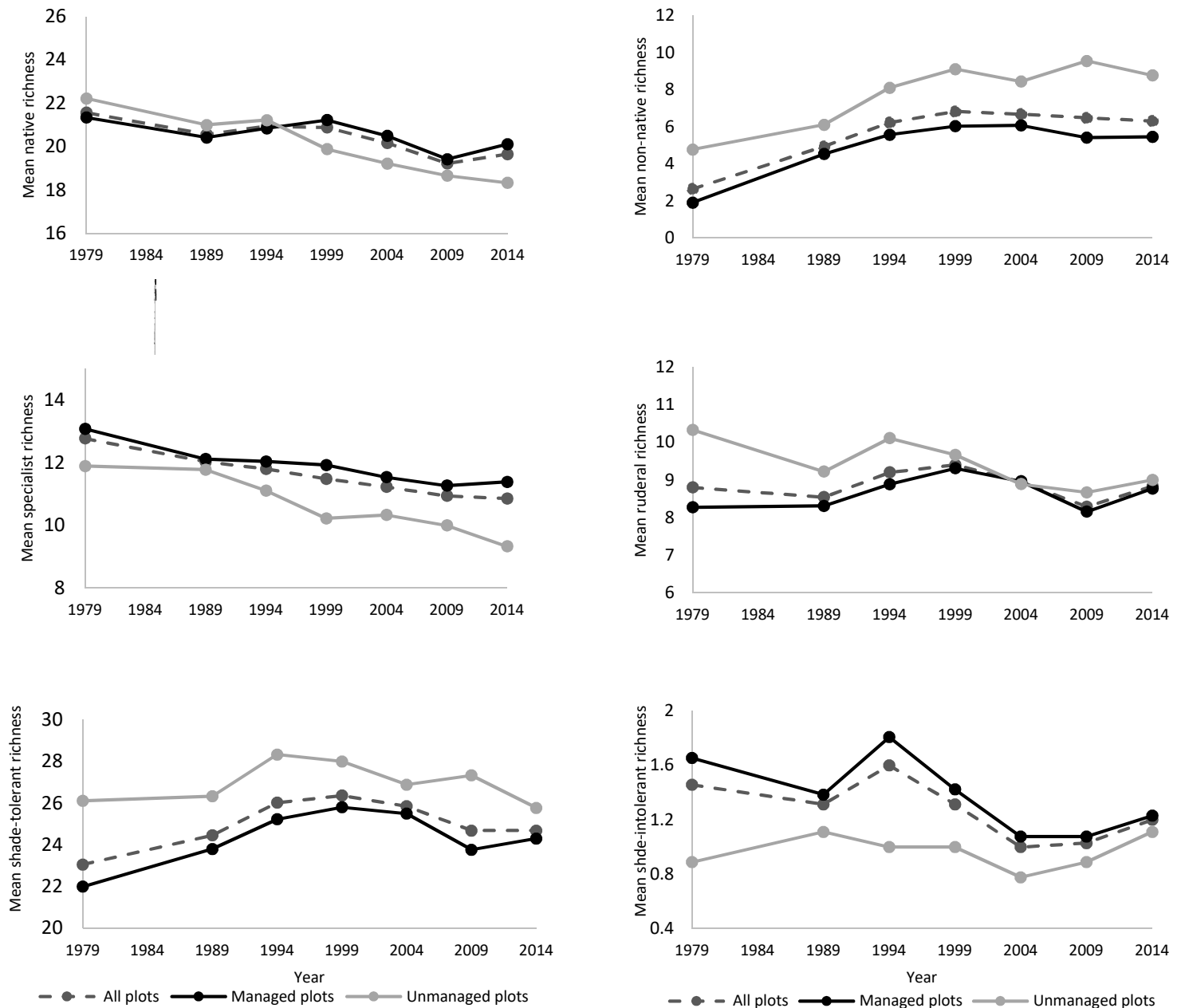


Figure 6. Temporal trends in mean richness per sample plot of particular groups of woody species: native, non-native, specialist, ruderal, shade-tolerant, shade-intolerant species.

Interestingly, forest communities did not become more homogenized over 35 years. This holds true for both managed and non-managed plots. Our results indicate that an increase in non-native species does not necessarily lead to biotic homogenization. Moreover, heterogeneous communities may not indicate high native diversity or healthy ecosystems. One important factor that might have contributed to heterogeneity in the unmanaged plots is the invasion history of the studied area. Specifically, non-native species that were introduced more recently and have lower residence time might have not achieved their potential range; they therefore increase floristic differentiation as opposed to non-native species introduced earlier (Lososová et al., 2012). In our case, we inform that biotic impoverishment is taking place despite the heterogeneous community composition.

Distance to agriculture and deer control frequency were important variables related to both non-native species abundance and richness. Although some studies have shown that roads and residential areas are important sources of non-native plants (Gelbard and Belnap, 2003; Borgmann and Rodewald, 2005; Maheu-Giroux and de Blois, 2007), agriculture was more influential than other land uses in our study. Agriculture provides resources such as nitrogen, which favors fast-growing species and can lead to their invasion or increased dominance (Huenneke et al., 1990). Furthermore, the agricultural lands near our forest preserves are older than the nearest roads and residential areas, and therefore may have had more time to contribute to the spread of non-native species. Jodin et al. (2008) found that road age is an important factor in common reed (*Phragmites australis*) invasion in Canada.

The positive effect of deer control in reducing non-native abundance and richness is in accordance with other studies that show non-native plant cover decreased in deer-proof plots (Nuzzo et al., 2017). Deer control can prevent dominance of the unpalatable, browse-tolerant

species (Goetsch et al., 2011) and non-native species that deer tend to avoid (Tesoriero, 2007) and can enhance native species vitality (Nasiri et al., 2017). In 25 of our research plots, deer control occurred more regularly and consistently compared to fire and clearing, which varied greatly from year to year. This may account for the greater contribution of deer management in controlling the non-native species. However, deer control may not be as effective in maintaining native species if the area has already been intensely browsed (Nuttall et al., 2014). Furthermore, lethal deer control can be limited by logistical constraints such as proximity to homes or other areas that are heavily used by humans.

3.6. Conclusion

Our study has implications for management and conservation. A positive finding is that biotic homogenization has not occurred in these urbanizing forest patches. In addition, the number of native species has not decreased. The vegetation management in our plots was able to slow down the spread of non-native species but did not prevent their increase over time. As shown in the NMDS results, managed plots appear to maintain the original community composition better than unmanaged plots. Vegetation management did not have a significant effect on shade-intolerant or ruderal species, but our data suggest a trend that might become significant with more time or more regular management. Therefore, we can conclude that fire and clearing are promising tools for preserving the woody plant communities in this region.

We suggest that if vegetation management was more consistent (repeated at regular intervals) it might have been even more effective in controlling the non-native species. It takes consecutive, repeated fires to stop seed production by killing existing individuals and eliminating plants that arise from the seed bank or from vegetative structures, which often are stimulated by

the initial fire (Dey and Kabrick, 2015). Wilhelm and Rericha (2007) show that implementation of fire and managed thinning on a regular basis resulted in a marked increase in native plant densities and diversity in Iowa (USA). Propagule reintroduction of native species may also help control the non-native species, as many native species may naturally be seed limited (Hartman and McCarthy, 2004). This method fills in the niches available after successful removal of non-native plants and prevents colonization and expansion of undesirable species (Kettenring and Adams, 2011). Nonetheless, non-native species control would not be fully effective in such a developed landscape unless it is extended to the neighboring environments (e.g., residential areas, city parks, street trees), so a collaborative public-private approach will be necessary (Webster et al., 2006).

Maintaining the diversity of native communities and controlling the spread of undesirable species have been recognized as priorities at the global level (Andersen et al., 2004). Our study provides insight into these important issues. Many different agents come into play for maintaining the native community; reaching this goal requires collaboration between forestry, research institutes and residents. By conducting more long-term studies and, ideally, more controlled and consistent management experiments, we will better understand the temporal dynamics of urban forests.

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CHAPTER FOUR

4. MODELING THE EFFECTS OF FIRE PRESCRIPTION AND DEER CONTROL ON OAK DOMINANCE IN URBAN FORESTS OF THE MIDWESTERN USA

4.1. Abstract

Restoring oak woodlands and other natural communities is a management priority in U.S. especially as there are some concerns regarding decline in oak species. Without effective restoration programs, this trend can eventually lead to loss of oaks in the future. In this study, I used the DuPage County empirical data along with model simulations to explore the management activities that maintain oaks and control the spread of oak competitors, especially sugar maple, over the next 100 years. Management scenarios included deer control, fire prescription, fire and deer control coupled, and no management. I also examined how structure (e.g. density and basal area of mature trees) and composition (dominance of oaks and other common tree species) would change over 100 years in different management scenarios. The results suggest that the importance value of red and white oak will not differ under different management scenarios. Fire combined with deer control may reduce sugar maple importance value compared to the no management and deer control scenario. However, sugar maple importance value will continue to increase under all management scenarios throughout time. Structural changes include a decrease in stem density and an increase in basal area over the simulation period. We conclude that there is a critical need for the removal of large sugar maple trees mechanically via thinning and cleaning to create a more oak-friendly environment.

4.2. Introduction

Throughout eastern and central North America, mixed-oak (*Quercus* spp.) forests are highly valued for many ecological and economic reasons (Brose et al 2013). They are a source of timber, food, habitat for wildlife, and they provide relatively open stand characteristics that promote diverse understory flora (Lashley et al 2011). Acorns alone provide a unique food source for over 100 vertebrate species in the eastern United States (Brose et al. 2014). Oaks are the most diverse genus in the United States and have been a dominant component of eastern forests for millennia (Delcourt and Delcourt, 1997). However, there has been a reduction in the dominance of oaks over the past two centuries. This has been due to fire suppression, land use change, high levels of deer herbivory, and competition with native and non-native invasive plant species (Whitney 1994, Abrams 2003). Reduction in oak abundance will have profound effects on species diversity and ecological processes (Knops et al. 1999). With the recognition that oaks are at risk, there has been a particular interest since the 1980s in conserving and restoring oak ecosystems (e.g., Abella et al. 2001; Hutchinson et al. 2012).

The exclusion of anthropogenic fire is a primary factor responsible for shifts of eastern oak forests to more shade tolerant species, especially maples. Many oak species currently in the canopy are long-lived, but widespread understory dominance by shade-tolerant species (Fralish and McArdle 2009) suggests that overstory composition of oak will continue to decrease. Moreover, the leaves and woody material of shade-tolerant species decompose faster than oak litter (Knoepp et al. 2005), decreasing fuel loads and retaining more soil moisture than co-occurring oak species, thereby potentially reducing flammability and creating more mesic site conditions that favor oak competitors (Nowacki and Abrams 2008). Consequently, oaks have declined in importance in many eastern forests (Knot et al 2019). Declines have been especially

marked in the Central Hardwood Region of the United States, which lost oak abundance on 81% of its forested area (169,968 km²) in less than 30 years (Fei et al 2011). Some studies predict that, without effective management treatments and restoration programs, white oak may nearly disappear in many of the remaining upland forest tracts within the next 50 to 100 years (Fralish 2004, Haas and Heske 2005) and be replaced by sugar maple and other shade tolerant species. Hence, finding the proper management and restoration methods to maintain oak ecosystems in the future is crucial.

Fire has been increasingly used as a restoration tool to promote the establishment and growth of oak. Fire is of particular importance to the development of larger competitive oak seedlings by controlling stem density and resultant light availability and reducing competition from non-oak species in the woody regeneration layer (Brose, 2014). Fire also controls excessive woody growth in general, as well as the growth of some non-native species that often are not adapted to burning (Anderson and Schwegman 1991, Nuzzo 1991). However, one potentially negative effect of burns is that the new shoots that emerge after a burn are more palatable and can attract deer (Hallisey and Wood 1976).

The early recovery and restoration of eastern deciduous forests may be impossible without deer management (Aronson and Handel 2011). Deer overpopulation may alter forest composition and structure by removing palatable species such as oaks and leaving the regeneration layer with less-preferred or browse-tolerant species such as *Fraxinus americana* or *Prunus serotina*, leading to declines in overall understory diversity and cover (Tilghman 1989; Knight et al. 2009). Russell et al. (2017) modeled recruitment dynamics of tree species in forests of the northern United States and showed that stands with very high browse impact would contain 50% fewer saplings and 17% fewer overstory trees. Many empirical studies have found

that survival and growth of seedlings and understory trees is higher in places where deer have been excluded or in areas with lower deer abundance (Aronson and Handel 2011; Shelton et al 2014; Owings et al 2017). However, deer management should be coupled with other management activities such as fire prescription and clearing, especially in areas that are highly invaded by shade-tolerant or non-native species.

Restoring oak woodlands and other natural communities is a management priority in the United States (Dey et al 2016). Predicting future structural changes under different management activities is essential to restoring native woodland biodiversity and ecological functions. Most field-based restoration studies have been carried out at relatively small temporal scales (typically a few years to less than 2 decades) (Jin et al 2018), but long-term projection is needed to see overall trends in composition and structural changes.

Our previous work in this system (Gharehaghaji et al 2019) concludes that there was lower non-native species richness in the managed plots. Although, further examination shows that this trend can not be attributed to management because non-native richness was initially lower in the managed plots (chapter five). In addition, over a 30-year period, we observed an increase in non-native species and a trend towards fewer specialist species and more shade-tolerant species. In the current study, we follow up on our previous work by integrating field monitoring data with model simulations to explore management activities that will improve the number of mature oak trees and control oak competitors such as sugar maple over the next 100 years. Making use of a long-term dataset collected in the suburban forest preserves of the Chicago metropolitan region (Illinois, USA), we ask the following research questions:

1. Will management activities in urban deciduous forests help improve the abundance and dominance of oaks in 100 years?

2. How will forest structure, including canopy cover and basal area, change under different management activities?
3. How will tree communities change over 100 years?

4.3. Methods

4.3.1. Study Area

The study area is DuPage County, Illinois, in the Midwestern region of the United States. DuPage County is in the Chicago metropolitan region and is the second most populated county in Illinois, with 916,924 people according to the US 2010 census (DuPage County Statistical Profile, 2011). DuPage County is mostly developed and suburbanized, although some pockets of farmland exist in the county's western and northern parts.

Historically, frequent fire controlled by Native Americans maintained prairie and oak savanna in much of the region (Bowles et al. 1994). However, today the region is generally amenable to the development of closed-canopy forests in the absence of frequent fires (Fahey et al, 2012). The average temperature ranges from a low of -10°C in January to a high of 23°C in July and average monthly precipitation ranges from 40 mm in February to 117 mm in August (based on climate normals from Illinois State Climatology).

We examined 35 plots located in 17 forest preserves that are managed by the county. The preserves themselves range from 7 ha to 1035 ha, but each plot was 0.45 ha. These plots are part of an existing long-term (from 1979 to today) monitoring program. Over the 35-year sampling period, 57 tree species have been identified in the plots, including 43 native and 14 non-native species (Gharehaghaji et al, 2019). In 2014, which is the most recent data available, the plots

were mostly comprised of white oak (*Quercus alba*), red oak (*Q. rubra*), bur oak (*Q. macrocarpa*), black oak (*Q. velutina*), wild black cherry (*Prunus serotina*), white ash (*Fraxinus americana*), American elm (*Ulmus americana*), sugar maple (*Acer sacharum*), and basswood (*Tilia americana*). In addition to white, red, bur, and black oaks, scarlet oak (*Q. coccinea*), and swamp white oak (*Q. bicolor*) have also been recorded in the plots.

Over the past 35 years, management in some plots has included deer control, prescribed fire, or both, while other plots were never managed at all. The management goals include reducing the number of invasive species and mesic tree species and promoting natural reproduction of oaks. Prescribed fire is usually applied in late fall or early spring before green-up. Fires are low intensity and mostly affect dead herbaceous vegetation and small shrubs and trees, but occasionally may affect mature trees. In plots managed by burns, the frequency of fire varies from every year to every 8 years. Deer control is practiced more regularly than prescribed burns and involves lethal removal to reduce the deer population to 6–8 individuals per square kilometer before fawning.

4.3.2. Woody Species Assessment

Between 1979-2014, sample plots were monitored every 5 years by DuPage County Forest Preserve field specialists. Starting in 1979, mature trees (diameter at breast height (DBH) ≥ 12.7 cm) were identified and counted in each site. In 2004, researchers began tagging mature trees and measuring their diameter at each sampling period. At that same time, researchers also began surveying saplings (< 7.62 cm DBH and > 100 cm height) and seedlings (< 2.54 cm DBH and < 100 cm height) in 5 (4m * 4 m) quadrats randomly placed in each plot. Dead trees and snags were also identified and measured for DBH from 2009 to 2014.

4.3.3. Modeling future forests

4.3.3.1. Forest Vegetation Simulator

To project the impacts of different management scenarios on the forest preserves, we used the Forest Vegetation Simulator (FVS), an individual growth and yield model developed by the U.S. Forest Service (Dixon 2002). Forest managers have used FVS extensively to summarize current stand conditions and predict future stand dynamics under various management scenarios (Krebs et al 2017). FVS has also been used to determine suitability of stands for wildlife habitat, estimate hazard ratings for insect outbreaks or wildfires, and predict losses caused by them (Seidl et al 2016; Lehman et al 2016; Ager et al 2020).

Model equations, such as those for tree growth and mortality are developed for specific geographic areas in the US and imbedded in the FVS framework. The FVS framework developed for a specific geographic area is called a geographic *variant* of FVS. For our particular purpose, we used the Central States variant of the FVS (Dixon and Keyser 2008). Each variant includes tree species that are typically found in the geographic region along with growth and mortality equations developed for that region. Mortality includes density-related mortality, which occurs when stands reach some level of density, and senescence of old trees. Mortality rates for individual trees are determined by a variant-dependent equation, but in general are higher for shade-intolerant species, smaller species (e.g. understory trees), and individual trees with less vigor (crown ratio) than their counterparts (Dixon 2002).

Despite its utility, FVS has several important limitations. One drawback is that, because growth-yield models focus on the production of merchantable timber (i.e., the growth of overstory trees), regeneration is not programmed in most variants (including the Central States

variant) and must be entered manually. In addition, FVS projects only native tree species, and does not include shrubs or non-native woody species. Despite these limitations, FVS has been used for over 30 years and is a suitable method for comparing structural dynamics under different management trajectories.

4.3.3.2. FVS Input

The vegetation data used as input for the FVS model are categorized into stand-level data or tree-level data. Stand (plot) input data are used to further adjust the model to site conditions and include geographic location, plot size, aspect, slope, elevation, forest type, and year inventoried. Tree-level data characterizes individual trees within plots and includes species identification, number of mature trees, saplings and seedlings, diameter at breast height (DBH), tree height, diameter growth, and age. FVS can estimate the height of large trees and the diameter of saplings and seedlings, based on diameter and height relations developed specifically for each species and variant (Dixon 2002).

For our analyses, each plot was considered to be a ‘stand’ in FVS and we examined each plot independently. The tree input included all large trees, saplings, seedlings, and dead trees that were observed in the 2014 survey. The only shrub included in our model was common buckthorn (*Rhamnus cathartica*), a non-native species that can grow to have a diameter more than 12.7 cm. Because FVS does not have codes for shrubs or non-native species, we represented buckthorn with the ‘Noncommercial species’ code. For each species, we calibrated diameter growth by measuring the diameter difference between all live trees in 2004 and 2014.

4.3.3.3. Regeneration settings

Because we were interested in examining changes in forest structure and composition over relatively long time periods, species regeneration was a crucial input for the FVS model. Although sprouting of certain species occurs automatically in the FVS model, users are responsible for providing estimates of natural seed-based regeneration in the Central States variant. To model regeneration in our plots, we selected representative plots that had experienced consistent management over the last 35 years. Five plots each were selected to represent four distinct management strategies, including deer control every year, prescribed fire every 3-5 years, both deer control and prescribed fire, and no management at all.

For each management strategy, we used the survey periods from the previous ten years (2004- 2014) from the five representative plots to calculate the average number of seedlings of each species that regenerate each cycle (Table XII, Appendix D). A projected cycle is a period for which tree and stand characteristics are predicted. We did not include regeneration from species that only occurred in one plot or where large parental trees were absent in the specific plots. Regeneration events were scheduled every ten years for the non-management and deer control scenarios, and every three years for fire and deer-fire scenarios. Therefore, because the number of seedlings regenerating was calculated for a ten-year period, we divided this number by 3.3 to enter the number of seedlings in a three-year cycle for the fire and deer-fire scenario. We allowed for sprouting to occur in each cycle for all scenarios.

4.3.3.4. Simulating management

We used FVS to predict forest structure over 100 years, under four different management scenarios (1) Deer control every year, (2) fire prescription in 3-year intervals, (3) Deer control (every year) and fire prescription in 3-year intervals, and (4) no management. When modeling

the different management scenarios, we assumed that all plots would be managed in the same way.

For the no-management and deer scenarios, we generated simulations from 2014 to 2114 with a 10-year cycle length. We accounted for the effect of deer control on oak seedlings by its effect on regeneration. Therefore, the only difference between these two scenarios was the regeneration input, which was based on empirical data as discussed above.

To model prescribed fire for the fire and deer-fire scenarios, we used the Fire and Fuel Extension (FFE) of FVS (Rebain et al 2010). Burn conditions, including temperature, wind speed, and date of fire, were recorded for all plots that were burned from 1985 to 2014. Based on the average environmental conditions for all prescribed fires in the last 20 years, we assumed that prescribed fires occur when temperatures are under 60° F (15.5 degrees C), conditions are moist, wind speed is approximately 14.5 km/hr, and before vegetation green-up. Prescribed fires were scheduled every three years, and we adjusted the fires to burn 15% of each plot, reflecting the typical mild prescribed fires that do not often open the canopy in DuPage County forests.

4.3.3.5. Model output and data analysis

For our analyses, we examined two output files from FVS. The first output file includes a list of tree species in each plot, which we used to calculate tree species richness. The second output file computes structural variables for all species combined and for each individual species. We used this output to evaluate and track total mature tree density, total basal area of mature trees, total canopy cover, and the number and basal area of mature red and white oaks and seven other common species: sugar maple, black cherry, white ash, American linden, American elm, bur oak, and black oak. All of the non-oak species are shade tolerant or have intermediate shade

tolerance. In addition, we evaluated number and basal area of black walnut (*Juglans nigra*) to represent shade-intolerant species, even though it is not common in our plots.

At each cycle, we calculated the importance value (IV) for mature oaks, the other common species, and black walnut. The IV of each species was the sum of relative density and relative basal area in each plot. Relative density was calculated as the number of stems per species divided by the total number of stems for all species, and relative basal area was defined as the basal area per species divided by the total basal area of all species combined; these numbers were converted to percentages by multiplying them by 100. Relative density and basal area each sum to 100 when all species are combined, and IV sums to 200. This index provides a measure of the relative dominance of a given species in a community (Strahan et al. 2016). The IV is commonly used in plant community analysis because it is not overly influenced by large trees or a large number of small trees from a particular species (McCune and Grace, 2002). The change in IV for each species over time was calculated by dividing its median IV in year 2114 by its median IV in 2014.

Models were run for 100 years. At the end of model runs, we compared the following metrics from each scenario: (1) the importance value of mature red and white oaks, other common species, and black walnut, (2) total density of mature trees in each plot, (3) total canopy cover of mature trees in each plot (4) total basal area of mature trees in each plot, (5) richness of mature tree species in each plot. As these variables were not normally distributed, we used Kruskal-Wallis test to compare these metrics under different management scenarios followed by post-hoc Dunn's test of multiple comparisons. All analyses were performed using R. Null hypothesis were refuted when $P \leq 0.05$ for the Kruskal-Wallis test and $P \leq 0.025$ for Dunn's test.

To better understand how tree populations are changing over time, we also examined red oak, white oak and sugar maple size classes among different scenarios. We categorized each individual of these species as a seedling (< 2.54 cm DBH), sapling (2.54-7.61 cm DBH), midstory tree (7.62-33.01 cm DBH), or overstory tree (≥ 33.02 cm DBH), and compared size class distribution after the 100 year simulations.

To visualize trends over time, we plotted total mature tree density, canopy cover, basal area, and richness over the 100-year period. We also show the ratio of change in importance value from 2014 to 2114 for all common species, and the size class distribution for red oaks, white oaks, and sugar maples.

4.4. Results

4.4.1. Structural change over time

Our projections show that density of mature trees will decline by approximately 60% over the next 100 years in all management scenarios. Similarly, median richness per plot is predicted to decrease in all management scenarios, by 2-3 species in 0.45 Ha (one acre). Conversely, basal area (m^2/ha) of all plots is expected to increase by 8.43-10.22 m^2/ha , depending on the scenario. Percent canopy cover is not predicted to change dramatically over time (Figure 7).

When comparing the four management scenarios, there was no difference in total canopy cover, total tree density, or richness (Table IX), but total basal area was slightly lower under fire and deer-fire scenarios (39.44 m^2/ha and 39.22 m^2/ha in median respectively) compared to no

management and deer management scenario (41.08 m²/ha and 41.02 m²/ha in median respectively) (Figure 7; Table XV, Appendix G).

4.4.2. Difference in species dominance under management scenarios

The importance value of red oak decreased over time in the non-fire scenarios and increased in the fire scenarios, but white oak increased in importance value over time in all scenarios (Figure 8). Kruskal-Wallis tests show that the importance values of red oak and white oak do not differ between any of the scenarios (Table IX). White oaks have higher importance than red oaks in 2014, and this remains true over the next 100 years in all scenarios (Table XIII, Appendix E). Sugar maple also increased in importance value over the 100 year simulations in all scenarios (Figure 8), and was higher in the no management scenario (median IV=35.78; $P<0.01$) and deer scenario (median IV= 31.99; $P=0.02$) than the deer-fire scenario (median IV=9.62) (Table XV, Appendix G). For all other common species and black walnut, importance values do not differ under the management scenarios (Table IX).

Most other species were predicted to have a lower importance value in 2114 compared to 2014 in all scenarios, although the median importance value of black walnut and black oak was 0 for both 2014 and 2114. The importance value of bur oak is expected to decrease dramatically in 2114 where it is 0 under the no fire scenarios and very low (median=0.20, median=0.21) under fire and deer-fire scenarios respectively (Figure 8). American linden is predicted to maintain 0.76-0.80 of its IV in 2114 under no fire scenarios.

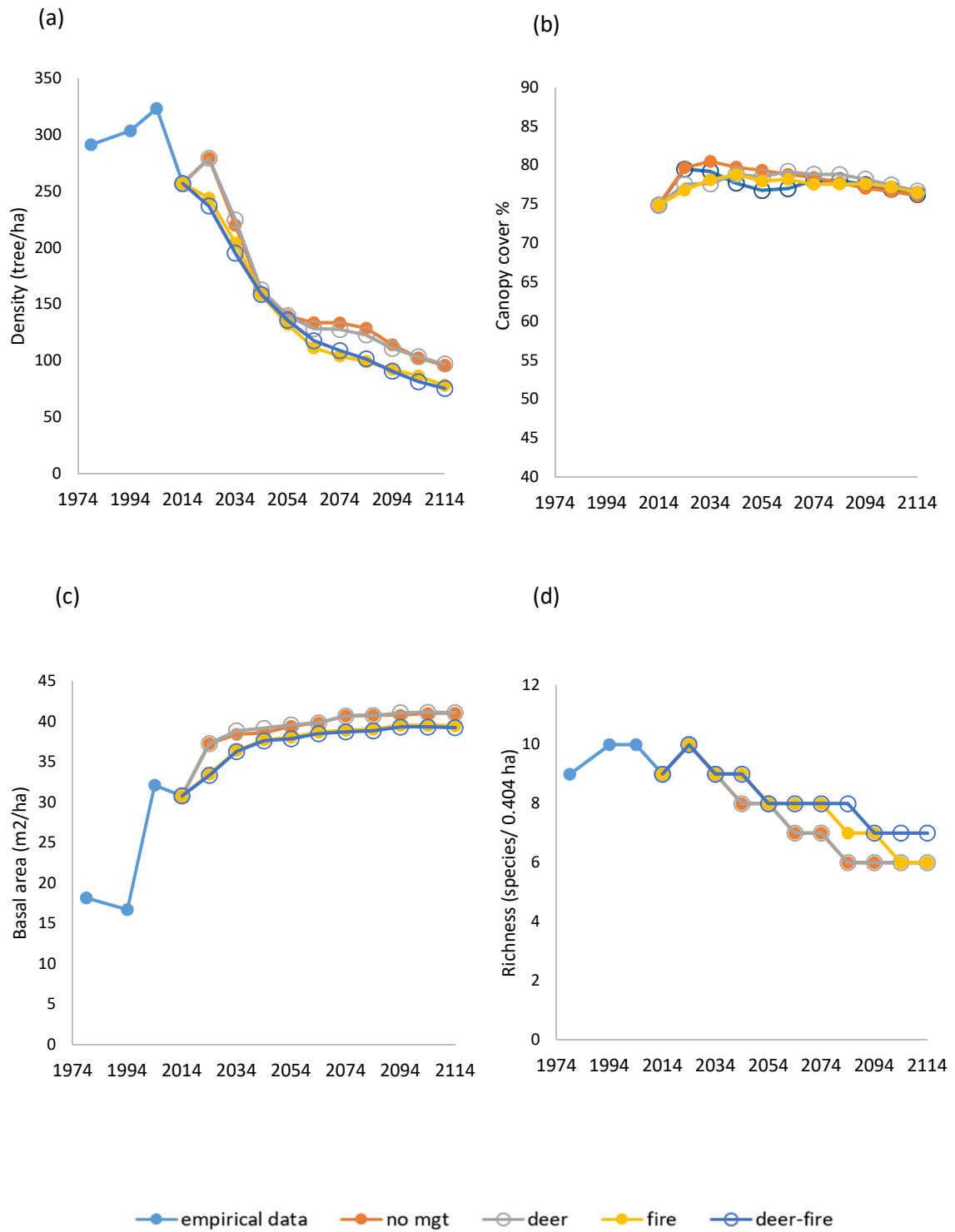


Figure 7. Changes in forest structure and richness from 2014 to 2114 under four different management scenarios within 35 forest plots in DuPage County, Illinois.

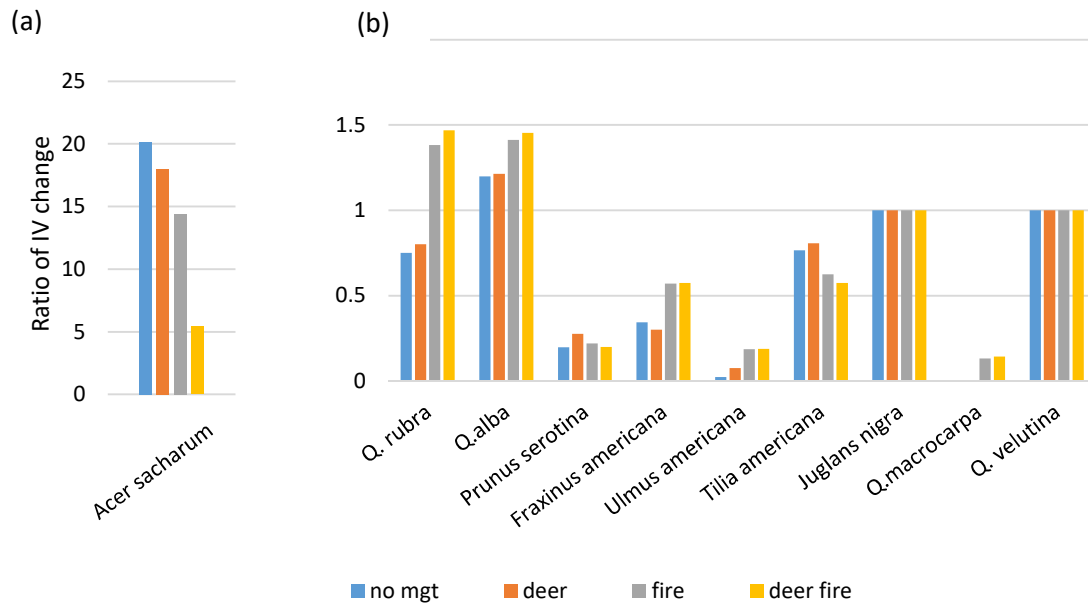


Figure 8. Ratio of change in importance value (IV) of (a) sugar maple and (b) other common species from year 2014 to year 2114. IV was calculated for each species by dividing the median IV in year 2114 by the median IV in 2014. Values < 1 indicate that the species decreased in importance value, while values > 1 indicate that the species increased in importance value. Black walnut and black oak had zero median IV in 2014 and 2114. Therefore, we decided that their ratio of change will be 0/0 equal to 1. Because of the large difference in change of sugar maple compared to other species, we show sugar maple change in IV on a separate graph. Sugar maple IV differs between no management and deer management scenario and deer-fire management.

Table IX. KRUSKAL-WALLIS TESTS COMPARING FOREST ATTRIBUTES BETWEEN FOUR DIFFERENT MANAGEMENT SCENARIOS AT THE END OF 100 YEAR SIMULATIONS. IV IS IMPORTANCE VALUE. EACH MODEL HAS 3 DEGREES OF FREEDOM.

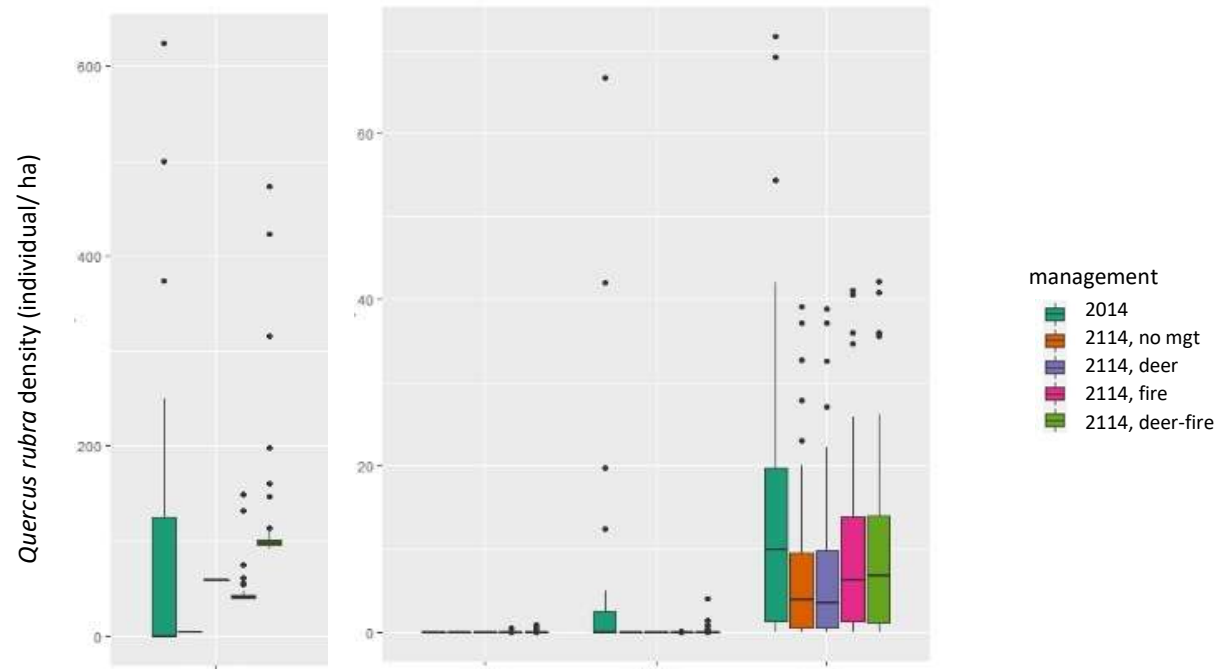
Response	Kruskal-Wallis chi-squared	P value
Tree density	6.449	0.091
Canopy cover	0.714	0.869
Basal area	10.188	0.017*
Richness	3.515	0.318
Red oak IV	4.196	0.241
White oak IV	4.364	0.224
Sugar maple IV	8.299	0.041*
Black cherry IV	0.273	0.965
White ash IV	5.268	0.153
American elm IV	2.360	0.501
American linden IV	0.713	0.870
Black walnut IV	3.012	0.389
Bur oak IV	1.625	0.653
Black oak IV	2.248	0.522

4.4.3. Size class analysis

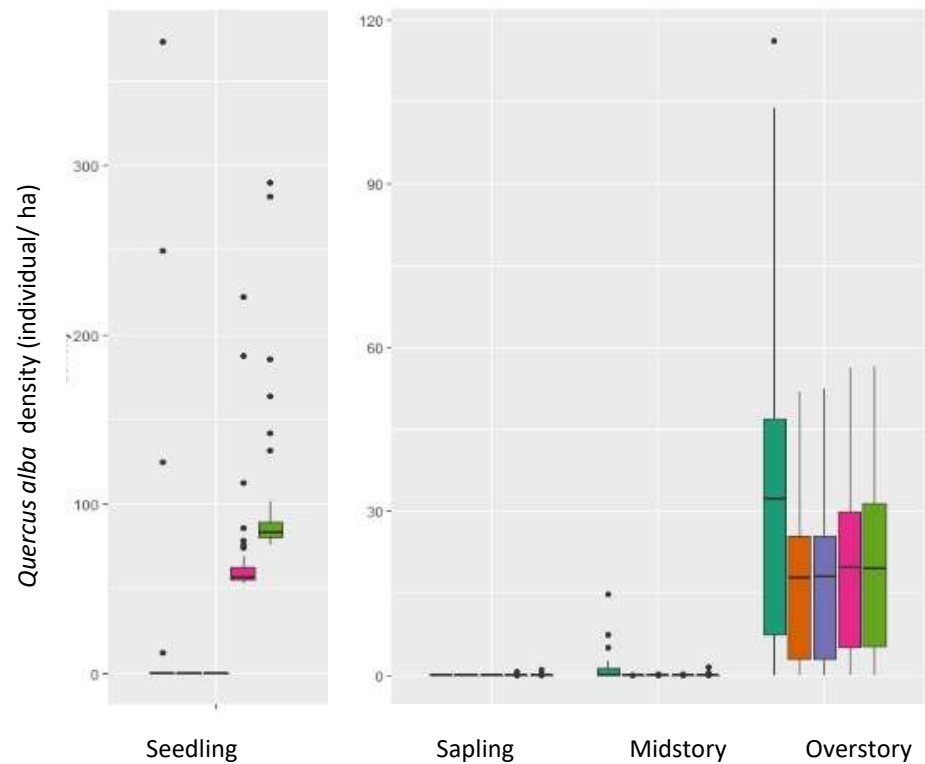
The size class distributions show an aging population for red and white oaks, with no sapling and few midstory individuals in most plots in 2014 and very few sapling and midstory in

2114 (Figure 9). This occurs despite a seedling cohort in most management scenarios. Sugar maples, on the other hand, are predicted to have numerous seedlings, saplings, and midstory individuals in all scenarios.

(a)



(b)



(c)

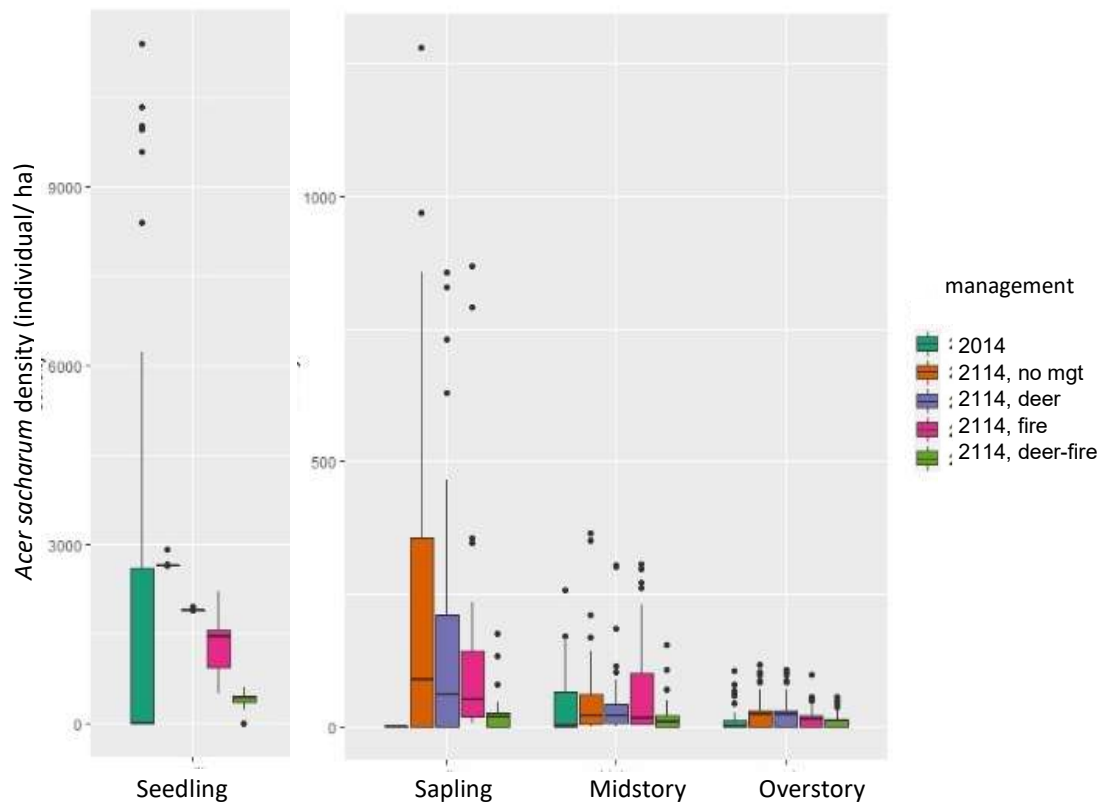


Figure 9. Density of (a) Red oak, (b) white oak and (c) sugar maple in different size classes under different management scenarios. Seedlings are plotted separately because of a much higher density than other classes.

4.5. Discussion

Long-term, empirical data on the effects of ecological management and restoration are rare. Thus, simulation models can provide valuable insight into future forest structure and composition change. In this study, we used simulation models to evaluate the long-term effects of fire and deer management on oak-dominated forests of the Midwestern United States. Our results suggest that management activities will have little impact on the importance values of red or white oaks, and will not increase the density of oak saplings or small trees over time. While

prescribed fire combined with deer control may effectively reduce sugar maple importance compared to no management and deer control scenarios, sugar maple importance value will continue to increase under all management scenarios throughout time. These results can help forest managers to reevaluate their management practices and make their decisions based on long-term outcomes.

Our models suggest that the structure and composition of these oak-dominated forests will change over the next 100 years. Although canopy cover did not change substantially over time in any of the management scenarios, stem density decreased and basal area increased over the simulation period. These changes make sense in light of the relatively young age of the forests (160- 200 years old; Bowles and Jones 2008). The decrease in density seems to be non-random and corresponds to a simultaneous, although less severe, decrease in species richness. Over the same time, most common species in our plots decreased dramatically in importance value. The two exceptions are sugar maple and American linden, both of which are very shade-tolerant. Based on their summed importance values, which total 140-150 out of a possible 200 (depending on the scenario), it appears that four tree species will dominate the composition of future forests in DuPage County: white oak, red oak, sugar maple, and American linden (Table XIV, Appendix F).

Red and white oaks are expected to remain dominant in the canopy for the next 100 years. They have the highest relative dominance (i.e., basal area) of the tree species that we examined, and their relative dominance is higher than their relative density (Table XIII, Appendix E). Therefore, their high importance values in all scenarios are mainly due to their basal area rather than the number of individual trees. Unfortunately, none of the management activities open the tree canopy or improve light levels to facilitate recruitment, and sapling and

midstory oaks are absent in the plots in 2114. Therefore, the sustained dominance of oaks is due to their long life spans and the persistence of old trees, and is unlikely to continue into the next century under current management regimes.

In contrast to the oaks, sugar maple density is expected to grow in all size classes under all management scenarios. However, the deer-fire management scenario is most effective in reducing sugar maple importance value. This outcome may be because the regeneration input file for deer-fire management had fewer sugar maple seedlings than input files for other management scenarios. Given that regeneration data are extracted from a limited number of plots, more studies of deer-fire interactions on controlling sugar maples would be beneficial. In all scenarios, sugar maple relative density will exceed relative dominance. As a result, the increasing importance value of sugar maple is mainly due to its relative density instead of basal area. Consequently, when the existing oak trees die off, there is a high chance that sugar maples will replace them due to their successful recruitment and understory dominance.

Our results suggest that deer management alone will not affect the forest structure nor importance value of oaks or sugar maple in our study area. There have been mixed results in studies that quantify deer impact on forest regeneration. Some show the positive effect of deer management in increasing oaks in the eastern US (Aronson & Handel 2011; Abrams 2013, Shelton et al 2014), while others show deer densities are not related to current tree densities and species trends (Hanberry & Abrams 2019 and Owings et al 2017). Hanberry et al (2020) concluded that competition from numerous fire-sensitive (e.g. sugar maple) tree species is a greater limiting factor for oak recruitment than deer browse. Therefore, deer control could be most effective in reducing competition from sugar maple and possibly improving oak recruitment when combined with other restoration practices (Thomas-Van Gundy et al 2014).

Other possible reasons for the apparent lack of effect of deer management are (1) deer control activities in DuPage County might not reduce deer numbers sufficiently, (2) current deer control may not be as effective in maintaining native species if the area has been heavily browsed in the past (Nuttle et al. 2014), or (3) the FVS model, as implemented in this study, does not capture the full effect of deer on vegetation dynamics. Currently, the model only implements an effect of deer by changing regeneration, but deer likely have other impacts not reflected in the model (e.g., on tree growth and mortality). We suggest that deer control should still be applied frequently in the study area because it effectively controlled non-native abundance and richness (Gharehaghaji et al 2019) and is expected to reduce sugar maple importance when coupled with fire.

The focus of this study was on the long-term effects of prescribed burning and deer control on oak-dominated forests. However, some factors that might affect ecological outcomes are not implemented in the FVS model. For example, the model does not account for mortality caused by insect pests or diseases such as oak wilt, which could cause premature deaths of trees. Oaks in DuPage County forests might not live as long as their life span in FVS suggests. Furthermore, FVS does not incorporate the effect of non-native species on tree growth or mortality, although we know they pose a critical threat to oaks (Schulte et al 2011) and other native plants (Vila et al. 2011). We suggest that, for our purposes, the FVS model might be most useful in providing a relative comparison between management scenarios rather than for its absolute predictions.

In conclusion, the ongoing management practices in DuPage County Forest Preserves might not maintain oak dominance over the long term. Using fire and other restoration tools to promote oak recruitment is a complicated task (Arthur et al 2012). Sustainable management of

oak forests requires long-term planning, careful monitoring, and flexibility in the timing and choice of management treatments (Mcshea et al. 2007). The constant increase of sugar maple density may decrease flammability of forests (Babl et al. 2020), making prescribed fire less effective in the future. Fire combined with mechanical thinning to reduce stand density could help reach a more oak friendly environment (Dey 2017) by stimulating germination, enhancing resource availability, and creating open spaces (Pyke et al. 2010, Willms et al 2017). Further research into the effect of thinning or canopy gaps in combination with fire and deer control will help understand their role in oak recruitment in our area.

4.6. Acknowledgements

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CHAPTER FIVE

5. CONCLUSION

In this dissertation, I have addressed some major concerns about oak-dominated forests. After evaluating current and future trends in non-native woody species richness and oak dominance, I conclude that the ongoing management does not seem effective in reducing non-native species richness, controlling shade-tolerant species (especially sugar maple), or enhancing oak recruitment. Therefore, oak conservation and management require strategic planning, long-term investments, and integral collaboration to deliver desired outcomes. Explicit modeling and simulations, by predicting future conditions under certain management practices, are helpful to evaluate and thereby improve management and restoration outcomes. In this chapter, I revisit some results from chapter three and discuss the effect of vegetation management on community composition. I also overview some potential management and restoration efforts to maintain resilient oak forest communities in the light of climate change, an important threat that affects oak-dominated landscapes in both the western and Midwestern US.

5.1. Revisiting community composition change

After careful examination of the effects of vegetation management on woody species composition in chapter three, I would like to slightly amend my conclusion to that published paper. I now conclude that, although managed plots are different in composition from unmanaged plots, there is no interaction between management and time. In other words, the managed plots were different in their composition from the beginning. Therefore, community changes over time cannot be attributed to management. Similarly, vegetation management did not affect any particular groups of woody species, including non-native species richness. The

nested GLMM results show that non-native richness is lower in managed plots. However, there is a lack of interaction between management and time. Therefore, I conclude that the reduction of non-native richness cannot be attributed to management, and non-native richness was initially lower in the managed plots.

A possible solution to control non-native species more efficiently may be regular clearing and thinning. This may be challenging due to the expenses and personnel required for clearing. In addition, long-term regular fire prescription applied *outside* the dormant season might help to advance oak woodland restoration and non-native species control (Vander Yacht et al. 2017). In our study area, prescribed fires are irregular and applied before greening to help fire containment but are less effective in controlling non-oak competitors (Keyser et al. 2017) and invasive species (Gruchy et al. 2009). Finally, integrating canopy disturbance through regular mechanical thinning and fire has more potential for controlling both non-native species and oak competitors (Dey et al. 2010).

Analysis of community change showed a clear shift in community composition over 35 years, but how this change affects ecosystem functionality, and thereby resilience, is unclear. This is because analyzing presence-absence of woody species does not reveal the change in ecological processes and functions. Despite their simplicity and wide application in ecological studies, incidence-based indices do not take species abundance into account, and thus abundant and rare species are treated equally (Chao et al. 2006). Nevertheless, even frequency-based analysis may not be sufficient to characterize community dissimilarities as they do not consider the biological (taxonomic) dissimilarity (Hao et al. 2019). Indices that include taxonomic hierarchies can better reveal the degree of biological relatedness of forest ecosystems, estimate the effects of habitat heterogeneity on community composition and diversity, and improve

assessment of species invasion or anthropogenic disturbance (Hao et al. 2019). Hence, it may be expected that the results of trait-or phylogeny-based studies could potentially provide a better understanding of biodiversity and ecosystem function relationships when compared with species-based approaches (Hao et al. 2018). Nevertheless, one can expect that given the increase in non-natives species richness over time, projected dominance of shade tolerant species, and lack of oak recruitment, ecological functions can deteriorate if proper management and restoration activities do not take place.

5.2. Climate change and recommendation for mitigation efforts

Climate change may complicate the effect of management and restoration practices and threaten the persistence of restricted endemic species (e.g. valley oak). Kueppers et al. (2005) used a fine-resolution regional climate model (RCM) to identify suitable habitat for valley oak populations in the future. The authors found that the potential range of valley oak will shrink considerably (54% of modern potential range size) by the end of the century and shift northward. They conclude that today's conservation areas may not protect future oak habitats. Valley oak's ability to shift its habitat range is constrained by fire regimes, browsing by domestic and wild animals, acorn predation, and competition with annual grasses and conifers (Welker & Menke 1990; Mensing 1992). On the other hand, local adaption may be less common than frequently assumed (Leimu & Fischer 2008). Moreover, long-lived organisms like trees are particularly vulnerable to maladaptation (adaptational lag to contemporary temperature) because of their long generation times (Gellie et al. 2016). Valley oak is already mismatched to the current temperature and will likely experience further declines in growth rates as temperatures rise over the next century (Browne et al. 2019).

Forests of the Midwest and Northeast US are also vulnerable to climate change (Brandt et al. 2014). Although oak species generally can tolerate hot and dry conditions, changes in precipitation patterns, disturbance regimes, soil moisture, pest and disease outbreaks, and non-native invasive species are expected to contribute to forest vulnerability across these regions (Swanston et al. 2018). Extreme precipitation may lead to more runoff, flooding, and nutrient inputs from surrounding agricultural areas (Janowiak et al. 2017), therefore favoring non-native species. Moreover, non-native species may do better in filling unoccupied niches during expected community range shifts (Vose et al. 2012). Increased spring precipitation gives rise to some pests such as bur oak blight in some parts of Illinois (Harrington et al. 2012). The fuel loads from pest-induced mortality, along with blowdown events, could further increase fire risk (Hicke et al. 2012). All this can lead to change in forest composition in bottomland forests (De Jager et al. 2016) and overwhelm management efforts to maintain native species diversity and resilience.

Developing and implementing techniques to abate these threats will require effective collaboration, creative research, and innovative management of the natural area to develop policy and management strategies ahead of time (Dunwiddie & Bakker 2011). Some overall recommendations for both western and Midwestern oak ecosystems include: (1) allowing a sufficient number of wild fires to burn along with prescribed fires to re-establish important ecological functions (Hamman et al. 2011), (2) employing deer management to keep the abundance in check (Frelich & Reich 2009), (3) mechanical thinning to control non-native species and restore oak-dominated ecosystems (Dey 2017), (4) focusing on detecting and eradicating newly-arrived invasive species (Dennehy et al. 2011), and (5) restoring highly degraded habitats to increase the acreage of native ecosystems, create buffers, and enhance

connectivity (Dunwiddie & Bakkar 2011). Large-scale restoration practices foster the creation of larger management units where fire and other ecosystem processes can be maintained at ecologically meaningful scales and where a greater range and quality of ecosystem services may be provided by oak ecosystems (Dunwiddie & Bakkar 2011). However, some recommended practices are challenging or even unrealistic in urban and suburban settings.

To ensure connectivity among valley oak populations and promote climate adaptation, mapping and conserving areas that facilitate movement (such as riverine ecosystems in the north) are critical (McRae et al. 2012). In addition, assisted gene flow seems a promising approach to mitigate the negative impacts of climate change (Browne et al. 2019). Using genomic approaches in a large-scale garden experiment, Browne et al. (2019) identified candidate genotypes in valley oaks that promote fast growth under warmer temperatures. Also, reintroduction of populations of Western bluebirds and other acorn dispersers to areas where they have been extirpated (Slater & Altman 2011) may enhance connectivity and range shifts for oak populations. Finally, as most oak-dominated stands are in private lands in California (Gaman & Firman 2006), identification of key parcels where the current extent, composition, and proximity to other priority habitats provide essential linkage, is essential for species conservation.

As mentioned before, active management of oaks can be complicated by the changing environmental, social, and economic conditions. For example, as the wildland-urban interface grows, prescribed burnings become increasingly difficult (Hamman et al. 2011). Also, controlling deer by culling and experimental fertility control programs are often disapproved by animal-rights agencies and the general public (Warren 2011). Moreover, how different disturbances might interact with each other under future climate scenarios is unclear (Dunwiddie & Bakker 2011). Nevertheless, the ability to predict restoration and management effectiveness

can be enhanced by carefully designed experiments replicated across many sites (e.g., Stanley et al. 2011) and fine-scale modeling that considers future species shifts (Dunwiddie & Bakker 2011).

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APPENDICES

Appendix A Table X

LIST OF THE WOODY SPECIES (TREES AND SHRUBS) FOUND IN DUPAGE COUNTY FOREST PRESERVE SAMPLE PLOTS BETWEEN 1979 AND 2014, ALONG WITH THEIR ASSIGNMENT TO PARTICULAR FUNCTIONAL GROUPS. COEFFICIENT OF CONSERVATION IS MEASURED ONLY FOR NATIVE SPECIES.

Woody species (tree and shrub) functional group	Common Name	Physiognomy
Native, shade tolerant, specialist species		
<i>Acer saccharum ssp. nigrum</i>	Black Maple	Tree
<i>Acer rubrum</i>	Red Maple	Tree
<i>Carya cordiformis</i>	Bitternut Hickory	Tree
<i>Carya ovata</i>	Shagbark Hickory	Tree
<i>Cercis canadensis</i>	Redbud	Tree
<i>Cornus alternifolia</i>	Pagoda Dogwood	Tree
<i>Crataegus calpodendron</i>	Sugar Hawthorn	Tree
<i>Crataegus coccinea</i>	Scarlet Hawthorn	Tree
<i>Crataegus flabellata</i>	Large-Seeded Hawthorn	Tree
<i>Crataegus pruinosa</i>	Frosted Hawthorn	Tree
<i>Crataegus succulenta</i>	Fleshy Hawthorn	Tree
<i>Fraxinus americana</i>	White Ash	Tree
<i>Fraxinus nigra</i>	Black Ash	Tree
<i>Fraxinus pennsylvanica</i>	Red Ash	Tree
<i>Fraxinus quadrangulata</i>	Blue Ash	Tree
<i>Ostrya virginiana</i>	Hop Hornbeam	Tree
<i>Pinus strobus</i>	White Pine	Tree
<i>Prunus americana</i>	Wild Plum	Tree
<i>Quercus alba</i>	White Oak	Tree
<i>Quercus bicolor</i>	Swamp White Oak	Tree
<i>Quercus macrocarpa</i>	Bur Oak	Tree
<i>Quercus rubra</i>	Red Oak	Tree
<i>Quercus velutina</i>	Black Oak	Tree
<i>Tilia americana</i>	American Linden	Tree
<i>Ulmus rubra</i>	Slippery Elm	Tree
<i>Cephalanthus occidentalis</i>	Buttonbush	Shrub
<i>Cornus amomum</i>	Blue-Fruited Dogwood	Shrub
<i>Corylus americana</i>	American Hazelnut	Shrub
<i>Euonymus atropurpureus</i>	Wahoo	Shrub
<i>Euonymus obovatus</i>	Running Strawberry Bush	Shrub

Appendix A Table X (continued)

LIST OF THE WOODY SPECIES (TREES AND SHRUBS) FOUND IN DUPAGE COUNTY FOREST PRESERVE SAMPLE PLOTS BETWEEN 1979 AND 2014, ALONG WITH THEIR ASSIGNMENT TO PARTICULAR FUNCTIONAL GROUPS. COEFFICIENT OF CONSERVATION IS MEASURED ONLY FOR NATIVE SPECIES.

Woody species (tree and shrub) functional group	Common Name	Physiognomy
Native, shade tolerant, specialist species (continued)		
<i>Ptelea trifoliata</i>	Wafer Ash	Shrub
<i>Ribes americanum</i>	Wild Black Currant	Shrub
<i>Ribes cynosbati</i>	Prickly Wild Gooseberry	Shrub
<i>Ribes missouriense</i>	Wild Gooseberry	Shrub
<i>Rosa carolina</i>	Pasture Rose	Shrub
<i>Rosa setigera</i>	Illinois Rose	Shrub
<i>Staphylea trifolia</i>	Bladdernut	Shrub
<i>Viburnum lentago</i>	Nannyberry	Shrub
<i>Viburnum prunifolium</i>	Black Haw	Shrub
<i>Viburnum rafinesquianum</i>	Downy Arrow-Wood	Shrub
Native, shade tolerant, ruderal species		
<i>Acer negundo</i>	Box Elder	Tree
<i>Acer saccharinum</i>	Silver Maple	Tree
<i>Acer saccharum</i>	Sugar Maple	Tree
<i>Celtis occidentalis</i>	Hackberry	Tree
<i>Crataegus mollis</i>	Downy Hawthorn	Tree
<i>Crataegus punctata</i>	Dotted Hawthorn	Tree
<i>Fraxinus pennsylvanica</i>	Green Ash	Tree
<i>Prunus serotina</i>	Wild Black Cherry	Tree
<i>Rhus typhina</i>	Staghorn Sumac	Tree
<i>Ulmus americana</i>	American Elm	Tree
<i>Cornus drummondii</i>	Rough-Leaved Dogwood	Shrub
<i>Cornus racemosa</i>	Gray Dogwood	Shrub
<i>Prunus virginiana</i>	Choke Cherry	Shrub
<i>Rhus glabra</i>	Smooth Sumac	Shrub
<i>Rubus allegheniensis</i>	Common Blackberry	Shrub
<i>Rubus flagellaris</i>	Common Dewberry	Shrub
<i>Rubus occidentalis</i>	Black Raspberry	Shrub
<i>Rubus pensilvanicus</i>	Yankee Blackberry	Shrub
<i>Sambucus canadensis</i>	Elderberry	Shrub
<i>Zanthoxylum americanum</i>	Prickly Ash	Shrub

Appendix A Table X (continued)

LIST OF THE WOODY SPECIES (TREES AND SHRUBS) FOUND IN DUPAGE COUNTY FOREST PRESERVE SAMPLE PLOTS BETWEEN 1979 AND 2014, ALONG WITH THEIR ASSIGNMENT TO PARTICULAR FUNCTIONAL GROUPS. COEFFICIENT OF CONSERVATION IS MEASURED ONLY FOR NATIVE SPECIES.

Woody species (tree and shrub) functional group	Common Name	Physiognomy
Native, shade-intolerant, specialist species		
<i>Juglans nigra</i>	Black Walnut	Tree
<i>Populus grandidentata</i>	Large-Toothed Aspen	Tree
<i>Quercus ellipsoidalis</i>	Hill Oak	Tree
<i>Quercus imbricaria</i>	Shingle Oak	Tree
<i>Salix nigra</i>	Black Willow	Tree
<i>Rosa blanda</i>	Early Wild Rose	Shrub
Native, shade-intolerant, ruderal species		
<i>Gleditsia triacanthos</i>	Honey Locust	Tree
<i>Malus ioensis</i>	Iowa Crab	Tree
<i>Populus deltoides</i>	Eastern Cottonwood	Tree
Non-native, shade-tolerant species		
<i>Abies concolor</i>	White Fir	Tree
<i>Acer ginnala</i>	Amur Maple	Tree
<i>Acer platanoides</i>	Norway Maple	Tree
<i>Catalpa speciosa</i>	Hardy Catalpa	Tree
<i>Crataegus monogyna</i>	Single-Seeded Hawthorn	Tree
<i>Malus baccata</i>	Siberian Crab	Tree
<i>Malus pumila</i>	Apple	Tree
<i>Malus sieboldii</i>	Japanese Crab	Tree
<i>Morus alba</i>	White Mulberry	Tree
<i>Phellodendron amurense</i>	Amur Cork Tree	Tree
<i>Ulmus X notha</i>	Hybrid Elm	Tree
<i>Berberis thunbergii</i>	Japanese Barberry	Shrub
<i>Euonymus alatus</i>	Burning Bush	Shrub
<i>Euonymus europaeus</i>	European Spindle Tree	Shrub
<i>Euonymus hamiltonianus</i>	Japanese Spindle Tree	Shrub
<i>Kochia scoparia</i>	Burning Bush	Shrub
<i>Ligustrum vulgare</i>	Common Privet	Shrub
<i>Lonicera maackii</i>	Amur Honeysuckle	Shrub
<i>Lonicera ruprechtiana</i>	Manchurian Honeysuckle	Shrub
<i>Lonicera X bella</i>	Showy Fly Honeysuckle	Shrub
<i>Lonicera X muendeniensis</i>	Common Fly Honeysuckle	Shrub

Appendix A Table X (continued)

LIST OF THE WOODY SPECIES (TREES AND SHRUBS) FOUND IN DUPAGE COUNTY FOREST PRESERVE SAMPLE PLOTS BETWEEN 1979 AND 2014, ALONG WITH THEIR ASSIGNMENT TO PARTICULAR FUNCTIONAL GROUPS. COEFFICIENT OF CONSERVATION IS MEASURED ONLY FOR NATIVE SPECIES.

Woody species (tree and shrub) functional group	Common Name	Physiognomy
Non-native, shade-tolerant species (continued)		
<i>Philadelphus coronarius</i>	Smooth Mock Orange	Shrub
<i>Rhamnus cathartica</i>	Common Buckthorn	Shrub
<i>Rhamnus frangula</i>	Glossy Buckthorn	Shrub
<i>Rosa multiflora</i>	Multiflora Rose	Shrub
<i>Symphoricarpos orbiculatus</i>	Coralberry	Shrub
<i>Viburnum opulus</i>	European Highbush Cranberry	Shrub
<i>Viburnum recognitum</i>	Smooth Arrow-Wood	Shrub
<i>Vinca minor</i>	Periwinkle	Shrub
Non-native, shade-intolerant species		
<i>Ailanthus altissima</i>	Tree Of Heaven	Tree
<i>Prunus subhirtella</i>	Higan Cherry	Tree
<i>Ulmus pumila</i>	Siberian Elm	Tree

Appendix B Table XI
EXPLANATORY VARIABLES USED IN GLMMS FOR NON-NATIVE ABUNDANCE AND RICHNESS

Variable	Details	Mean (min-max)	Source
<i>Local-level variables</i>			
% slope	Dominant slope inside the forest plot (2003)	15.77 (1.60-33.80)	Illinois Statewide 30-Meter Digital Elevation Model http://www.isgs.illinois.edu/
Aspect	Aspect inside the forest plot (2003)	Mode: South	Illinois Statewide 30-Meter Digital Elevation Model http://www.isgs.illinois.edu/
% clay	Year 2002 data	22.46 (19.70-37.00)	Soil Survey Geographic database (SSURGO)
% soil organic matter	Year 2002 data	2.13 (1.12-5.00)	Soil Survey Geographic database (SSURGO)
% Light	Measured with photographer's light meter (2014)	4.68 (0.52-40.50)	Field data
Initial native tree and shrub richness	Based on 1979 community data. Measured by counting the number of native trees and shrubs in each plot	19.65 (12-25)	Field data
Pre-settlement vegetation type	Original land cover (forest or other non-forested cover) in 1821-1840	Mode: Forest	Bowles et al. (1998)
<i>Management variables</i>			
Burn frequency	Number of managed burns from 1979-2014	3.60 (0-12)	Field data
Clearing frequency	Number of clearings from 1979-2014	0.80 (0-4)	Field data
Deer control frequency	Number of deer culling events in the surrounding forest preserve between 1979-2014	8.17 (0-21)	Field data
Vegetation management	Distinguishes between plots that have had any direct manipulation of vegetation (burns or clearing) and those that have not	Mode: Managed	Field data

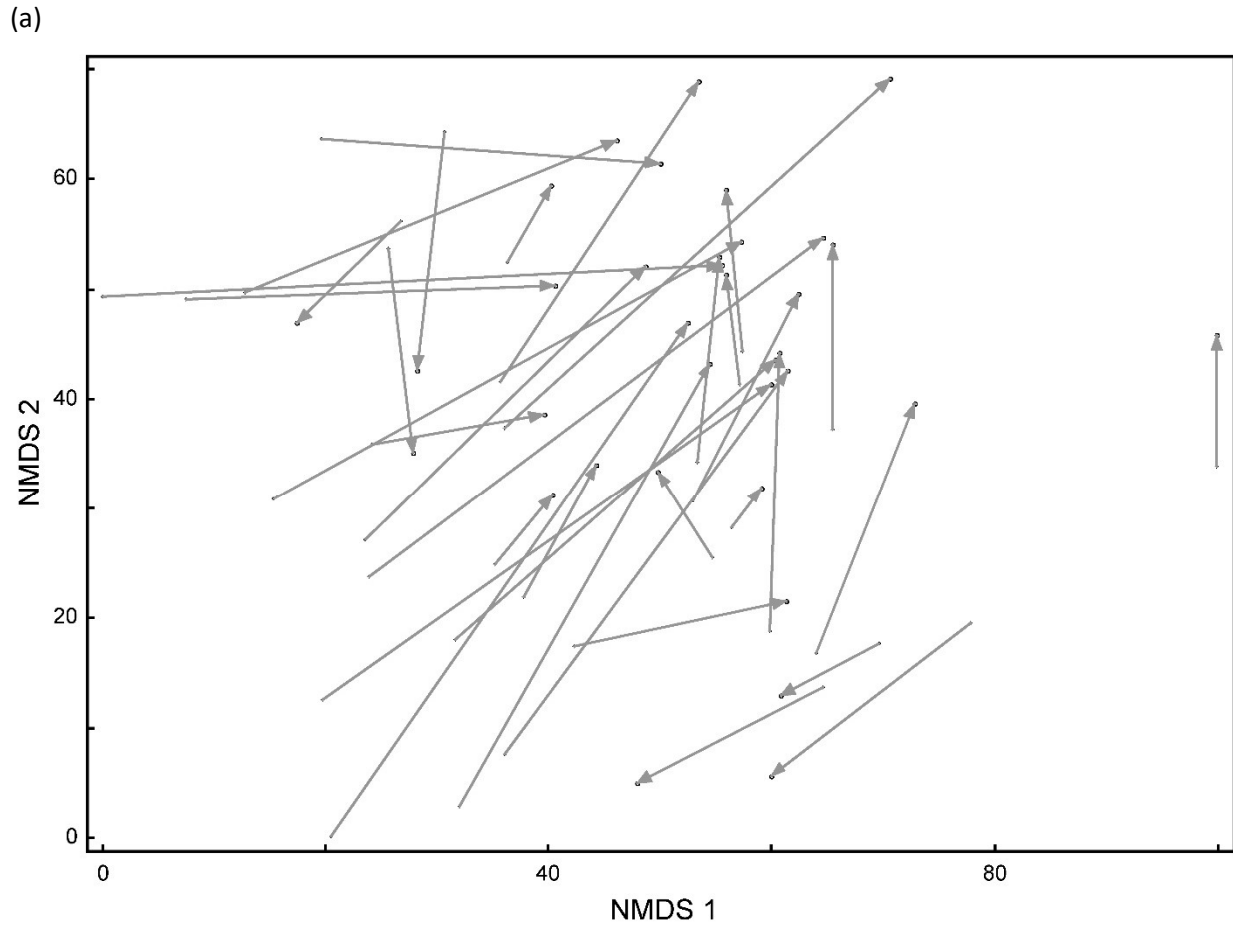
Appendix B Table XI (continued)

EXPLANATORY VARIABLES USED IN GLMMS FOR NON-NATIVE ABUNDANCE AND RICHNESS

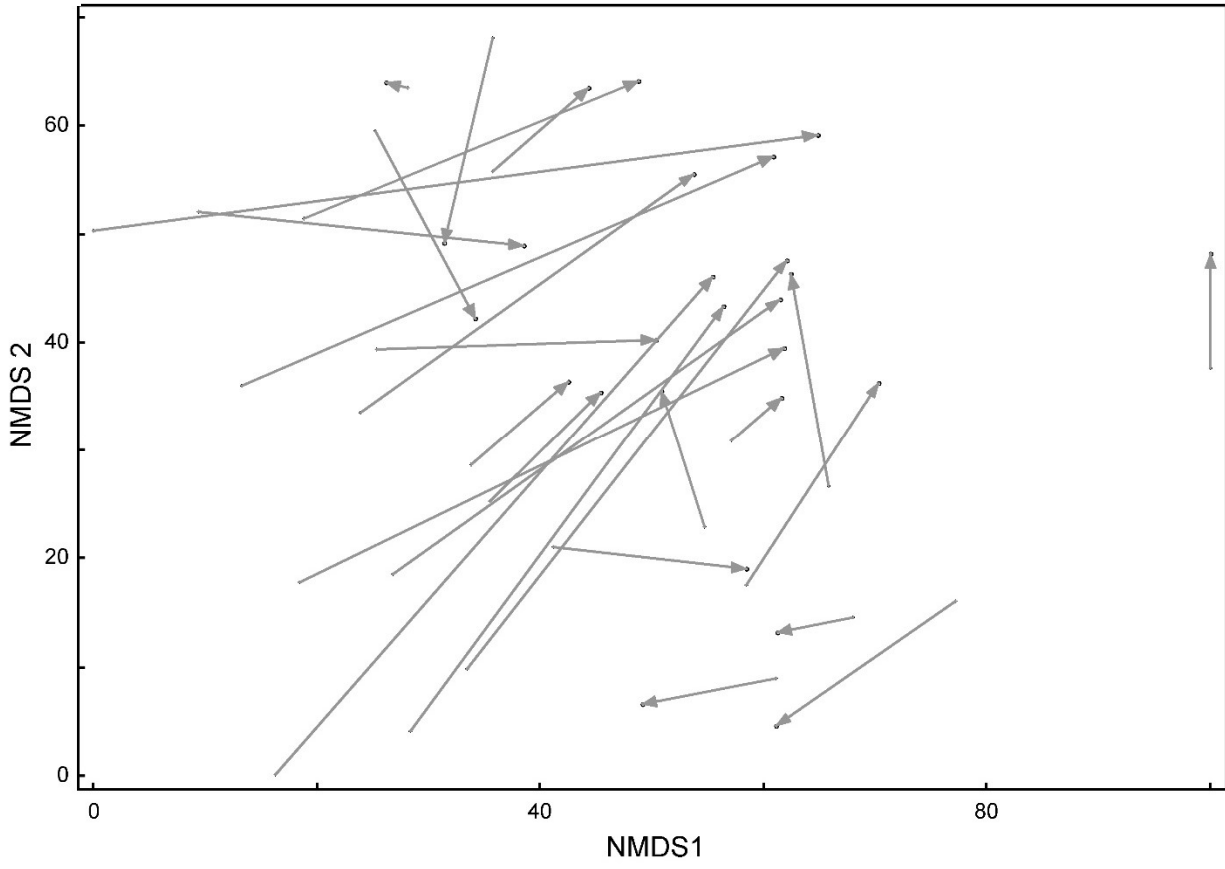
Variable	Details	Mean (min-max)	Source
<i>Landscape-level</i>			
% Canopy cover	Measured in 500 meter buffer around the center of each plot.	49.91 (7.60-95.13)	National Land Cover Dataset (NLCD) 2011
Distance to forest edge	Distance from center of plot to the forest edge	133.30 m (7.00-345.00)	National Land Cover Dataset (NLCD) 2011
Distance to road or trail	Distance from center of plot to nearest paved road or trail	137.20 m (15.00-374.00)	ArcGIS basemap
Distance to nearest residential area	Distance from center of plot to the nearest residential land	338.90 m (41.93-1170.00)	Chicago Metropolitan Agency for Planning's (CMAP) 2013 Land Use Inventory for Northeastern Illinois
Distance to agriculture	Distance from center of plot to nearest agriculture land cover	2289.00 m (260.40-7283.00)	National Land Cover Dataset (NLCD) 2011
Distance to river	Distance from center of each plot to nearest river	403.83 m (25.41-1652.12)	National Hydrography Dataset (NHD) year 2013

Appendix C Figure 10

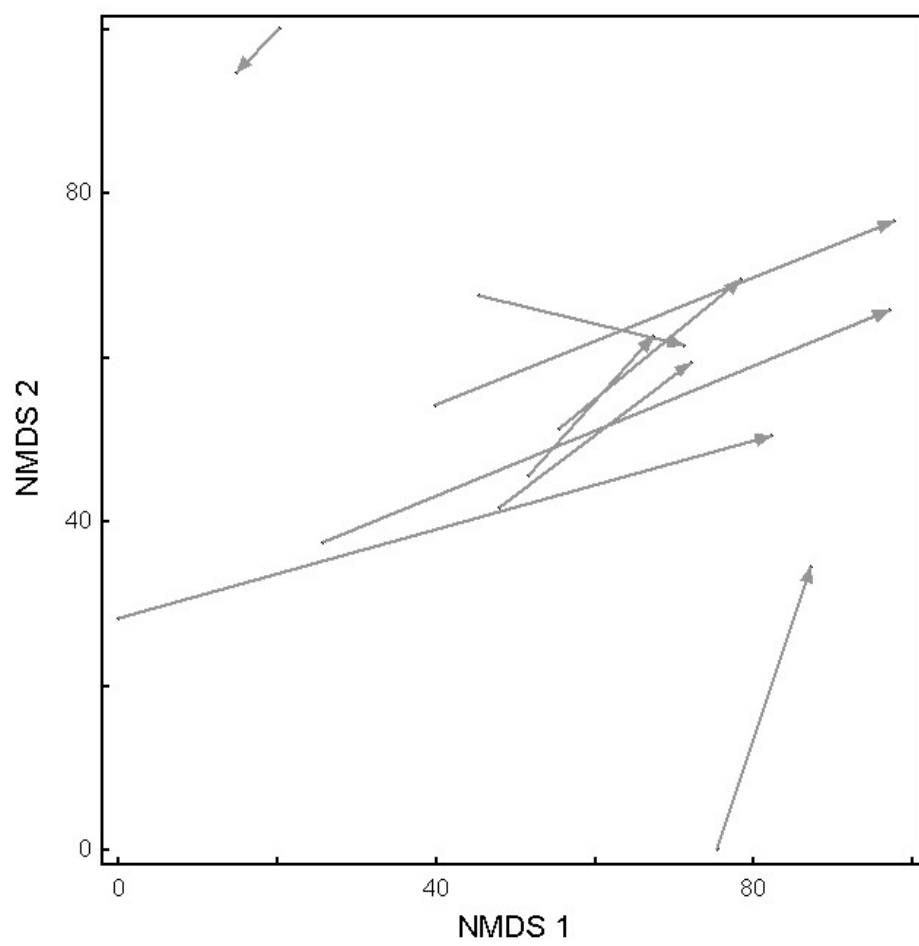
Changes in community composition showed by successional vectors for a) all plots
b) managed plots c) unmanaged plots. Successional vectors show the pairwise trend between
1979 and 2014 plots, with the arrow pointing from 1979 to 2014.



(b)



(c)



Appendix D Table XII
 EMPIRICAL SEEDLING ABUNDANCE PER 0.45 HA (1 ACRE) UNDER DIFFERENT
 MANAGEMENT SCENARIOS, BASED ON AVERAGE SEEDLING DATA IN
 REPRESENTATIVE PLOTS FROM 2004-2014. THESE DATA ARE USED IN THE FVS
 REGENERATION INPUT FILES. THE REGENERATION NUMBERS FOR ALL
 SCENARIOS ARE PER 10 YEARS FOR EASIER COMPARISON.

Species	No management	Deer management	Fire management	Deer-fire management
American Elm <i>Ulmus americana</i>	41	38	59	62
American Linden <i>Tilia americana</i>	71	60	-	200
Bitternut Hickory <i>Carya cordiformis</i>	-	120	125	266
Black Oak <i>Quercus velutina</i>	-	-	-	66
Black Walnut <i>Juglans nigra</i>	-	13	-	6
Box Elder <i>Acer negundo</i>	44	-	29	99
Common Buckthorn <i>Rhamnus cathartica</i>	643	160	201	53
Hackberry <i>Celtis occidentalis</i>	24	26	33	33
Hop Hornbeam <i>Ostrya virginiana</i>	-	54	-	261
Red Oak <i>Quercus rubra</i>	5	80	49	118
Shagbark Hickory <i>Carya ovata</i>	-	74	267	313
Slippery Elm <i>Ulmus rubra</i>	-	26	23	23
Sugar Maple <i>Acer saccharum</i>	1070	767	580	396
White Ash <i>Fraxinus americana</i>	1124	900	891	957
White Oak <i>Quercus alba</i>	-	-	66	99
Wild Black Cherry <i>Prunus serotina</i>	165	124	274	214

Appendix E Table XIII
RELATIVE DENSITY (R DEN), RELATIVE DOMINANCE (R DOM) AND MEDIAN
IMPORTANCE VALUE AMONG 35 PLOTS (IV %) FOR OAKS AND OTHER COMMON
SPECIES IN YEAR 2014 AND 2114 UNDER DIFFERENT MANAGEMENT SCENARIOS.

	2014			2114, No management			2114, Deer management			2114, Fire management			2114, Deer-fire management		
Species	R den	R dom	IV	R den	R dom	IV	R den	R dom	IV	R den	R dom	IV	R den	R dom	IV
<i>Q. rubra</i>	3.8	12.2	16.0	3.5	10.0	12.0	3.6	9.8	12.8	7.3	22.2	22.1	7.3	16.5	23.5
<i>Q. alba</i>	12.5	29.1	42.4	14.6	27.2	50.8	17.8	26.8	51.4	23.9	33.7	59.9	25.8	33.1	61.6
<i>Acer sacharum</i>	1.2	0.2	1.8	33.3	6.5	35.8	25.9	4.7	32.0	21.3	12.4	25.6	8.0	0.7	9.6
<i>Prunus serotina</i>	6.4	2.8	11.6	1.3	1.0	2.3	1.6	0.8	3.2	1.2	2.1	2.6	1.4	0.6	2.3
<i>Fraxinus americana</i>	3.1	3.5	7.0	0.8	1.6	2.4	0.8	1.4	2.1	1.3	3.5	4.0	1.7	2.7	4.0
<i>Ulmus americana</i>	2.1	0.7	3.0	0.0	0.0	0.1	0.1	0.1	0.2	0.2	1.2	0.6	0.2	0.3	0.6
<i>Tilia americana</i>	6.9	4.0	12.0	4.8	3.7	9.2	5.6	4.0	9.7	5.3	7.2	7.5	3.4	2.0	6.9
<i>Juglans nigra</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0
<i>Q. macrocarpa</i>	0.6	0.7	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.1	8.0	0.2	0.1	0.1	0.2
<i>Q. velutina</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.5	0.0	0.0	0.0	0.0

Appendix F Table XIV

RELATIVE DENSITY (R DEN), RELATIVE DOMINANCE (R DOM) AND AVERAGE IMPORTANCE VALUE AMONG 35 PLOTS (IV %) FOR OAKS AND OTHER COMMON SPECIES IN YEAR 2014 AND 2114 UNDER DIFFERENT MANAGEMENT SCENARIOS. IN 2014 FOUR SPECIES OF RED AND WHITE OAK, SUGAR MAPLE AND AMERICAN LINDEN MADE UP 122.4 OF THE TOTAL IV (200) BUT IN 2114 IT IS EXPECTED THAT THIS VALUE WILL INCREASE TO 139.63-150.29 DEPENDING ON THE SCENARIO.

Species	2014			2114, No management			2114, Deer management			2114, Fire management			2114, Deer-fire management		
	R den	R dom	IV	R den	R dom	IV	R den	R dom	IV	R den	R dom	IV	R den	R dom	IV
<i>Q. rubra</i>	8.3	16.4	24.6	7.6	17.0	24.6	7.7	16.9	24.6	10.3	22.2	32.5	10.4	22.0	32.4
<i>Q. alba</i>	14.3	29.6	44.0	14.3	28.2	42.4	14.8	28.4	43.3	18.9	33.7	52.6	20.2	34.6	54.7
<i>Acer sacharum</i>	16.3	11.7	28.0	34.1	21.8	55.8	31.7	21.4	53.1	27.2	12.5	39.6	23.0	11.2	34.2
<i>Prunus serotina</i>	13.4	6.8	20.1	5.3	4.0	9.3	6.0	4.1	10.1	3.6	2.1	5.6	3.5	2.0	5.4
<i>Fraxinus americana</i>	4.2	3.7	7.9	1.2	2.2	3.3	1.2	2.1	3.3	1.9	3.5	5.4	2.1	3.6	5.6
<i>Ulmus americana</i>	4.7	2.1	6.8	0.7	1.0	1.7	0.6	1.0	1.7	0.9	1.2	2.1	0.8	1.1	1.9
<i>Tilia americana</i>	16.0	9.9	25.9	15.0	12.5	27.5	14.2	12.4	26.6	9.2	7.2	16.4	10.2	8.1	18.3
<i>Juglans nigra</i>	1.9	1.9	3.8	0.8	1.1	1.9	0.9	1.0	1.9	1.0	1.1	2.1	1.1	1.1	2.1
<i>Q. macrocarpa</i>	5.4	10.8	16.1	1.5	4.9	6.4	1.5	4.9	6.5	2.5	8.0	10.4	2.9	7.5	10.4
<i>Q. velutina</i>	2.7	2.2	4.9	1.5	2.2	3.7	1.7	2.2	3.9	2.3	2.5	4.8	2.3	2.5	4.8

Appendix G Table XV

RESULTS OF DUNN POSTHOC TESTS SUGGEST THAT SUGAR MAPLE IMPORTANCE VALUE WILL BE LOWER IN THE DEER-FIRE SCENARIO COMPARED TO NO MANAGEMENT AND DEER CONTROL SCENARIOS, AND BASAL AREA OF ALL TREES WILL BE LOWER IN BOTH FIRE SCENARIOS.. THE FIRST VALUE IS Z-TEST STATISTICS AND THE SECOND VALUE IS *P*. FOR THE FUNCTION "DUNN.TEST" NULL HYPOTHESIS IS REFUTED WHEN $P < 0.025$.

Response variable	no management, deer management	no management, fire management	no management, deer-fire management	deer management, fire management	deer management, deer-fire management	fire management, deer-fire management
Sugar maple (IV)	-0.356577 0.3607	-1.747522 0.0403	-2.357534 0.0092*	1.390945 0.0821	2.000957 0.0227*	-0.610011 0.2709
Basal area	0.082513 0.4671	-2.277967 0.0114*	-2.148303 0.0158*	2.360481 0.0091*	2.230816 0.0128*	0.129664 0.4484

* $\alpha = 0.05$, Reject H_0 if $p \leq \alpha/2$

Appendix H

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Gharehaghaji, M., Kobal, S., Reklau, R. and Minor, E.S., 2019. Management slows down invasion by non-native plants but does not prevent community change over 35 years in urban forests of the Midwestern USA. *Forest Ecology and Management*, 448, pp.424-431.

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