NORTHWESTERN UNIVERSITY

Impacts of Restoration and Management on Plant Communities and Belowground Processes in the Chicago Region

A DISSERTATION

SUBMITTED TO THE GRADUATE SCHOOL

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS

for the degree

DOCTOR OF PHILOSOPHY

Field of Plant Biology and Conservation

By

Lauren Glyndal Umek

EVANSTON, ILLINOIS

March 2018

Abstract

Ecological restoration is a land management tool for biological conservation in areas where ecosystems are subject to a suite of natural and anthropogenic disturbances. This approach is particularly critical in urban areas where disturbances are often frequent and substantial. Restoration projects aim to re-establish an entire ecosystem, including the native organisms as well as the ecological processes and biotic interactions of those ecosystems for long-term sustainability. In practice, ecological restoration has primarily focused on establishing a diverse plant community while largely ignoring the belowground components of ecosystems. Surprisingly little is known about the complex relationships between soil factors, plant communities, and ecosystem processes in pristine systems, and even less is known about these relationships in restored or urban systems. In my dissertation, I ask: how do aboveground-focused management practices influence plant communities and belowground processes in the Chicago region?

I address this question using research that spans spatial and temporal scales and includes different terrestrial habitats. I examine ecological patterns of restoration activities at sites replicated across a large landscape, plant-soil interactions at the site level, and interactions between plant tissues and fungal communities using molecular techniques. I also address these questions across temporal scales. Using a restoration chronosequence, I use a space for time substitution to investigate ecological patterns over large periods of time. In a manipulative field study, I examine plant-soil dynamics over a period of 4 years. My study sites include private and publicly owned lands that represent a range of upland terrestrial habitats in the Midwestern U.S. and are managed by citizen scientists, government agencies, and professional contractors and combinations therein. My highly replicated, regionally comprehensive, and ecologically and

politically representative experimental approach ensures that conclusions from my research have direct and immediate impacts on the understanding of these ecosystems and how they are managed.

In Chapter 1, I describe the development of a collaborative network of protected sites that capitalize on the shared best management practices in the Chicago region. This network links on-the-ground restoration and land management activities with ecological research. This chapter provides the conceptual and experimental framework as well as experimental methods for collecting baseline data used in the subsequent studies. In Chapter 2, I describe how patterns in plant community structure and soil nutrient levels in woodlands and prairies differ with management duration and relate to one another. I found that in prairies, land use history is the most important factor in determining plant community assemblage followed by more recent land management activities. In woodlands, the initial action of removing woody invasive taxa is critical to initiating ecosystem restoration, while on-going management maintains community composition. In Chapter 3, I used geospatial analysis to develop a model of woodland degradation that integrates invasive shrub density, exotic earthworm biomass, and soil nitrogen availability. Using this model, I found that unrestored sites have significantly higher invasive shrub cover, exotic earthworm biomass, and soil nitrogen availability than managed sites, regardless of their time under management. I also identified notable exceptions to these patterns that may be used to direct and prioritize future investigations and ultimately, lead to more cost-effective restoration efforts. In Chapter 4, I examine the decomposition rates of leaf litter in remnant and former row-crop agricultural prairie ecosystems across the restoration chronosequence and describe the functional and community composition of the decomposer fungal communities. I found that leaf chemistry was a more important driver of litter mass loss than either land use history or management duration. I also found that although fungal communities differed in composition, they remained functionally similar across all sites. In Chapter 5, I conducted a manipulative field experiment exploring traditional and novel methods of restoration following the invasion of a non-native shrub (*Rhamnus cathartica*). I determined that amending soils with woody mulch following buckthorn removal significantly reduced reinvasion over the four-year field study period but that these results are not due to a reduction in soil nitrogen availability. Manipulative studies in the greenhouse similarly showed that mulch-amended soils significantly reduced buckthorn germination, seedling growth, and transplanted sapling growth. The results of this study suggest that incorporation of ground woody material into the soil following aboveground removal may facilitate restoration following European buckthorn invasion.

In this dissertation, I set out to examine and document how aboveground-focused management practices influence plant communities and belowground processes in the Chicago region. My research shows that land management practices influence plant community composition and soil nutrient availability across a range of ecosystem types. From a landscape perspective, these results are important in that they demonstrate that local correlations between above and belowground communities differ from those on the broader scale. From an applied perspective, my research informs land management practice and restoration of temperate woodlands and globally threatened tallgrass ecosystems, but also contributes to our knowledge on the processes and interactions between plant and soil communities that determine biological diversity in the Midwest US, especially in urban ecosystems.

Table of contents

List of tables and figures

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 1

Developing a long-term ecological research program in an urban area: The Chicago Wilderness Land Management Research Program

Abstract

The Chicago Wilderness Land Management Research Program (CWLMRP), more affectionately known as "100 Sites for 100 Years," is an experimental network that connects cutting-edge applied and theoretical ecological research with on-the-ground land-management practices. This cross-disciplinary research program connects land managers and academic researchers in restored and managed sites across four counties within the Chicago Wilderness (CW) region with the goal of addressing key questions about the impacts of management activities on organisms and ecological processes. Since the initiation of the CWLMRP in 2008, I have identified 121 one-hectare sites of woodland, savanna, prairie remnants, and prairie restorations in former agricultural fields that are replicated across a management gradient. These sites include degraded, unmanaged sites, restored and managed sites, as well as areas identified by managers as high-quality reference sites. In this chapter, I discuss the history and establishment of the network, its goals and theoretical framework, and describe the methodologies for collecting the baseline data that comprise the foundation for subsequent chapters.

Introduction

Ecological restoration is the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (SER 2004). It is a particularly important conservation strategy in urban areas, where lands are subject to a wide range of anthropogenic impacts including hydrological changes, habitat fragmentation, altered fire regimes, invasive species, loss of structural diversity, and ecosystem nutrient loading, all of which can adversely impact protected lands and waters (Heneghan et al. 2012). The goal of ecological restoration is to shift an ecosystem towards a state that is resilient and self-sustaining with respect to species composition and ecosystem structure and function. Restoration methods must also be technically achievable and socially acceptable so that efforts are beneficial for both landowners and biodiversity (Gobster 1997, Perring et al. 2015). There are a variety of conceptual frameworks and practical methods for developing restoration and management programs based on ecological principles and supported by empirical evidence or data modeling (Michener 1997, Hobbs 2007, Heneghan et al. 2008a, Heneghan et al. 2008b). In practice, however, the inherent complexities of restoration and idiosyncrasies of each site mean that efforts to restore areas can be met with very mixed results (Blumenthal et al. 2003a, Moore et al. 2006, Palmer et al. 2010). This outcome makes it challenging to identify sites and landscapes within which restoration efforts are needed or likely to be successful. Further, practitioners now desire a much stronger ecological foundation for developing and managing restoration projects.

Theoretical frameworks are increasingly important to understanding the symptoms and drivers that indicate an ecosystem in need of restoration versus a target or reference ecosystem, and identifying attainable restoration milestones and goals. Similarly, the monitoring of restoration success is problematic because the nominal objectives and accepted attributes are simplistic (e.g., diversity), highly subjective (e.g., community structure, function), site specific, occur over a short time frame (e.g., 1- 5 years after restoration), and rarely include a control (Allen et al. 1997, Michener 1997). Integrating the theory and practice of restoration thus requires a coordinated, multidisciplinary approach.

Land managers in the CW region have been developing, employing and improving best management practices for restoring terrestrial ecosystems for several decades (Helford 2000). However, there has been no coordinated effort on a regional scale to document, describe, or quantify the impacts of restoration efforts on soil properties and plant communities over time, or provide ecological descriptions of ecosystems that are considered by land managers to be degraded versus those that are more self-sustaining and high-quality. In this chapter, I develop a long-term, landscape-scale, replicated natural experiment that serves as a framework for future studies to investigate impacts of ecological restoration practices in the Chicago region. This research program provides the foundation for Chapters 2 – 4 of this dissertation.

Chicago Wilderness

Chicago Wilderness is regional alliance of more than 340 urban conservation organizations, federal, state, and local agencies, public and private land-owners, conservation organizations, corporations, and scientific, cultural, religious and educational institutions that work together to restore local nature and improve the quality of life for all who live in the greater Chicago metropolitan region. Chicago Wilderness also describes nearly 150,000 hectares of protected open-space across four states (Chicago Wilderness, 2016) including habitats of biodiversity conservation interest such as tallgrass prairie, oak savanna, and woodlands (Samson and Knopf

1996, Manning et al. 2006). This alliance represents a unique approach in conservation as it recognizes the human element of conservation in addition to the value of nature. This interaction has received international recognition and been the subject of academic case studies for environmental conservation in urban areas (Brawn and Stotz 2001, Heneghan et al. 2012). In particular, the organizations and work of the CW region have been recognized in the significance of CW members' contributions to the field of ecological restoration and restoration ecology (Woodworth, 2013). The work of the alliance has emphasized the importance of ecological restoration as a core conservation strategy, focused on initiatives to recover the region's biodiversity, and developed strategies for achieving conservation goals (Council 1999). Despite the accomplishments and acknowledgements of the applied conservation work of the CW Alliance, quantitative evaluations of these actions, and especially those aimed at meeting conservation goals, have been minimal.

Historically, there has been an unproductive and large disconnect between the work of restoration practitioners and the work of researchers despite the recognized centrality of restoration practice (Young et al. 2005). This disconnect has some potentially grave consequences, since practitioners are often disappointed by the outcome of their efforts, and researchers often pursue more esoteric issues at the expense of local applied research. The CWLMRP thus builds upon a solid collaborative foundation, bringing together managers, researchers, and restoration volunteers to circumvent this disconnect.

One of the most significant accomplishments of the CW Alliance is arguably the development and implementation of a region-wide standardized set of 'best management practices' in ecological restoration. These practices have been developed over decades of observation, applied research, adaptive management, case studies, and anecdotal information from knowledgeable volunteers and professionals. Typically, this approach starts with the removal of invasive species through mechanical (cutting or pulling) or chemical (herbicide) treatments. Initial removal is typically followed by treatment of missed stems, resprouts, and emerging individuals, and cultural management (prescribed fire), depending on site conditions. Native species are then introduced, typically through broadcast seeding or planting of plugs, and managed over time through mowing and/or fire. Specific tools and methods (loppers and bow saws, chain saws or heavy equipment) and the intensity and duration of restoration activities varies according to available resources and perceived needs of the site by practitioners. This approach is consistent with the practices of adaptive management. Fortunately, the regional implementation of standardized restoration and management has resulted in a replicated, natural experiment throughout the Chicago region that facilitates the study of restoration and management in key terrestrial habitats.

Chicago is recognized as a hub of cultural, historical, political and scientific institutions. Despite the prevalence of world-class museums, universities and research institutes in the region, there has yet to be a venue that fosters a constructive collaboration between the practical and empirical factions of the conservation community. As a result, I developed a cross-disciplinary research program that connects on-the-ground land management efforts across the region to applied and theoretical ecological research. One tangible result of the development of this research network is the increased value added to the local ecological research community, detailed in Appendix A. The data collected within this context is also intended to not only answer immediate applied ecological questions about relationships between land management and biodiversity, but also provides a highly replicated baseline for future examinations of site-specific or landscape trends throughout the region.

Management Categories

My study sites represent the region's major terrestrial systems: woodlands, tallgrass prairie remnants, and former row-crop prairie restorations (hereafter, restorations). Detailed definitions of these terms are given below. Sites were classified by land managers as being representative of one of four management categories: degraded/unmanaged, recently restored (< 10 years ago), intermediate restorations (restored and managed for at least 10 years), and reference sites (detailed below).

Within this framework, it became clear that there was a need to include unique sites that might not necessarily meet the general expectation of a positive relationship between management efforts and ecological outcomes. Such exceptions include sites that are not biologically diverse but are also not heavily degraded through invasion. Additionally, this category also includes the occurrence of highly diverse but unmanaged areas with minor to moderate invasive species presence. Although rare, sites with such incongruent conditions are intriguing and could provide insights that enhance our understanding of the relationship between management, plant community assemblage, and invasion dynamics.

Sites

The sites selected for the research program occur along a gradient of management duration and thus constitute a space-for-time experimental design (Table 1). Site managers were responsible for identifying and classifying suitable study sites into management duration categories, ensuring that any research conducted was complimentary and did not interfere with other agency activities, management goals and priorities, or public information sharing guidelines. Inclusion in the program also assumed that the site would be visited at least annually, and perhaps more frequently for more intensive studies. The ecological concentration of sites included in this program area was initially limited to key terrestrial ecosystems, although the expansion to wetlands, aquatic or other habitat types is a future goal.

The end result is a network of 121 research sites across the Chicago Wilderness region (Figure 1) that represent woodland, savanna, and prairie habitats that have been selected along a gradient of restoration or management duration. Sites are replicated throughout four counties (Cook, Lake, DuPage, and McHenry) in the Chicago region. The goal was to identify at least 24 study sites per county – three replicates each of the control, early, and intermediate management categories for woodlands and prairie restorations, and one of each management category for prairie remnants, as well as at least one reference site for each of the three habitat types (Table 1). Each site represents a separate management unit, even though several management units may be present in a single preserve. For example, one woodland preserve may include three management units and thus three study sites that fall into different management categories: one area that was cleared and seeded 15 years ago (intermediate), another area that was restored three years ago (early), and an additional area where substantial restoration has not yet occurred (unmanged/control). Further, one preserve may contain two areas that were cleared of invasive shrubs and seeded at the same time, but are burned and managed as separate units to facilitate habitat refuges and preserve-scale diversity. These sites would then serve as replicates for the same habitat type and management category. This site selection and replication process generally ensures that each plot represents an independent unit for the purposes of statistical analysis. While the study area size requirements will vary depending on the organisms and/or processes of interest, and may be smaller or larger within the unit, all sites are at least one-hectare and the center point of the study site is determined randomly within the management unit.

Basic Site Properties

Key baseline properties were collected and organized for all sites. This information included: overall preserve site name, specific site name, habitat type, management category, and GPS location of the center point of each site. This information was recorded in a sharable spreadsheet and geospatial database. For simplicity, sites were universally abbreviated to indicate habitat type and management category. For example, SiteName Z# where Z referred to the habitat type (W = woodland, P = prairie remnant, R = prairie restoration) and # referred to the management category (0 = control/unmanaged, 1 = early, 2 = intermediate, 3 = reference). Because navigation to the 1 hectare site within each preserve can be particularly challenging, the center point of each plot, was saved in an editable, shareable Google Earth (.kmz) file, labeled using the site abbreviation along with "tips for the field" information. This format provided a rapid way to determine spatial arrangement of study sites and select sites for field studies. For example, the location of the site relative to the lab may be important for time-sensitive experimental analyses. The shared format also allowed potential collaborators to access data from mobile or stationary electronic devices regardless of geospatial software knowledge and experience.

The "tips for the field" comprised practical information for accessing each site including site access restrictions (e.g., open 9am-5pm, no one permitted off trail during spring migration), visit notification requirements (e.g., call non-emergency police prior to visiting), most efficient parking and access routes, as well as notes on field conditions and recommended gear, (e.g., "will walk through dense *Rosaceae* spp. patches, wear heavy pants"; "path to site may be flooded in spring, bring tall boots"). These tips, while not necessarily ecologically vital, facilitate more efficient field visits. In addition, any available information on land acquisition history, restoration and management history, other significant activities (e.g., farming, recreation activities), notable characteristics, or other studies conducted on the site are included and available for collaborators.

The collection of photos from set points was also identified as being important in site documentation because photos quickly and easily capture the general condition of a site. The value of historical photos in modern management has also proven highly valuable. Based on the long-term vision of this project, baseline historical photos of each site were taken at the center point of each site, at breast height (1.4m) in each of the cardinal directions.

Vegetation structure and function

Vegetation analysis was conducted using a modified Whittaker plot method (Figure 2). All trees greater than 2.54 cm diameter within nine 100m^2 circles were identified to genus and species where possible and the diameter at breast height (DBH) was measured. In addition, all large trees (> 60 cm DBH) outside of the 100m^2 sampling plot but within the hectare site were identified, measured, and given an approximate location (e.g., approx. 15m NW of NW plot). These trees were included as they contributed to the overall structure of the site, canopy cover of the plot, and seed source throughout the site.

All shrubs within nine 4-m^2 quadrats were identified to genus and species where possible and counted by height class (0.5-1.0 m, 1.0-1.4 m and >1.4 m). Vegetation cover was estimated using the Braun-Blanquet classification system in these nine 4-m^2 quadrats using functional plant groups: trees, invasive woody, invasive herbaceous, herbaceous plants, moss, woody debris, leaf litter, and bare ground. Vegetation analysis in prairies followed a similar plot design with functional groups of non-native forbs, non-native grasses, native forbs, native grasses, sedges and rushes, woody stems, detritus, moss, and bare ground. Any species that was dominant within a plot (> 5% cover) was identified to genus or species where possible and the cover class recorded.

Canopy openness, a measurement of canopy structure and a proxy for light availability, was determined using five fisheye photographs taken at breast height and at ground level at five of the nine vegetation plots (center and each of the four cardinal directions) and analyzed using Gap Light Analyzer 2.0 software (Figure 3).

Soil factors

Replicate soil cores each measuring approximately 7-cm in diameter and 10-cm deep were collected from each site at approximately 10-m away from the center point, and transported to the lab in a Ziplock bag in a cooler.

Large debris and visible organic material was removed from each core and the soil was analyzed for moisture content, pH, texture (particle size) as well as total carbon (C) and nitrogen (N). Laboratory procedures for this analysis follow the methods used by the United States Long Term Ecological Research (U.S. LTER) Network (Robertson et al. 1999).

Soil nutrient availability was determined using commercially available ion exchange membranes called Plant Root Simulator™ probes (hereafter, PRS™ probes) (Johnson et al. 2007). PRS™ probes measure soil nutrient supply with minimal soil disturbance and can provide cumulative information about plant-soil interactions across a variety of soil types and over time. Two sets of PRS™ probes (two cation, two anion) were buried near the center of each study plot for 28 days (Figure 4). The PRS™ probes were returned to the supplier for analysis of soil ammonium (NH_4^+), nitrate (NO_3^-), phosphate ($H_2PO_4^-$, HPO_4^{2-}), potassium (K^+), calcium (Ca^{2+}), magnesium (Mg^{2+}), sulfate (SO_4^{2-}), iron (Fe^{2-}), aluminum (Al^{3+}), manganese (Mn^{2+}), copper (Cu^{2+}), zinc (Zn^{2+}), boron (B^{3+}), and lead (Pb^{2+}) as µg nutrient per cm2 over 28 days. All measurements were taken during peak growing season (from mid-June to late-August) in 2009-2012.

What's in a name? 100 Sites for 100 Years

An important element of the Chicago Wilderness Land Management Research Program is its long term perspective. Most studies only provide a snapshot of community dynamics as directed by grant periods, student schedules, and academic review cycles. However, it is increasingly recognized that many questions in biology, ecology, ecosystem science, and evolutionary biology can only be addressed with long-term data (Callahan 1984, Lindenmayer and Likens 2009). This is because many organisms have extended life-spans or turnover times longer than the length of most studies. In addition, plant and soil nutrient pools can turn over at longer term time scales, as do external forces such as climate change.

While the formal name for the program is the Chicago Wilderness Land Management Research Program, this program is more commonly referred to as “100 Sites for 100 Years.” This name is preferable, in that it immediately demonstrates the large-scale, replicated nature of the program (100 Sites). Although there are now 121 study sites in the program, some turnover of sites is expected as land-management practices and priorities shift, but there is a general expectation that the number of replicates will remain close to and, more often than not, exceed the 100 sites. The “100 Years” component of the title implies the long-term approach of the program. In addition, the types and methods of data collection in the formative years of the project were deliberately chosen to ensure they could be readily replicated over time and broad enough to show general trends over space and time, but still sufficiently detailed to provide ecological insights. Notably, the sites and program were intentionally designed to out-live the careers and life-spans of the original PIs and ecologists.

Terminology

Restoration – Ecological restoration is the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (SER, 2004). While this term could be used to describe all types of management activities, since all protected natural areas within the Chicago region (and arguably, the planet) could be described as degraded or damaged, this term refers to the initial, substantial resources investment employed to promote a shift in ecosystem function from a highly degraded or damaged state to a more desirable condition. For example, the conversion of a dense thicket of European buckthorn (*R. cathartica*) to an open oak (*Quercus* spp.) savanna would be considered an act of ecological “restoration,” whereas the maintenance activities of a similar ecosystem but without a significant presence of invasive shrubs would referred to as "management."

Management – Often used in conjunction with "restoration," this term refers to the on-going maintenance activities that sustain and/or improve ecological conditions of a given site. This term is often used as a substitute for "restoration" in higher quality sites where the goal is to maintain, enhance, or improve the biodiversity, plant community structure, habitat quality, or ecosystem function. It is distinguished from restoration because the term does not imply the transition of a given site "from x to y" as restoration often does to municipalities and the general public. For example, the term "management" is often preferred when referring to the ongoing physical or chemical removal of invasive plants and introduction of periodic prescribed fire in the maintenance of an oak woodland as opposed to the term "restoration,"

Unmanaged – This term, also referred to as "invaded," "degraded" or "control," depending on the context, refers to sites in this category were not actively managed at the start of the program. A woodland in this category is usually dominated by the invasive species, *Rhamnus cathartica*, *Lonicera maackii*, and/or *Alliaria petiolate*.

The unmanaged equivalent for grasslands are those sites no-longer in agricultural production and are minimally managed by mowing but with no immediate plans for tallgrass prairie restoration. These sites may be categorized as old-field sites in some counties. Generally, they are dominated by Eurasian grasses (e.g., *Agrostis gigantia*, *Poa* spp., *Echinochloa crus-galli, Phleum pretense, and Dactylis glomerata*) and legumes (e.g., *Melilotus* spp., *Trifolium* spp., and *Securigera varia*). In remnant grasslands, these unmanaged sites more closely resemble the plant communities of unmanaged woodlands, where the community is often dominated by woody European taxa (e.g., *R. cathartica, Cornus* spp, and *Frangula alnus, and L*. maackii) rather than herbaceous species.

The use of this term also implies that there are no plans for management or restoration activities in these sites, at least in the short term. Interestingly, these sites were the most difficult for land managers to select. This difficulty perhaps stems from the acknowledgement that resources for management are insufficient and, despite their ambitions and long-term restoration and conservation goals, the site would likely persist in its current, unmanaged state. However, these sites are included because they are a considered to be a relatively low priority for conservation purposes. These sites also function as a short or long-term control when investigating the impacts of restoration and land management activity on a key organism, community or process, and hold value in defining degradation, degraded conditions or potential changes in species composition or ecosystem function over time in the absence of management.

Woodland – Woodland sites are areas with approximately 25-50% tree canopy cover.

Prairie remnant – The distinction between a prairie remnant and prairie restoration emerged after a conversation early in the development of the project and experimental design process with a land manager in one of the participating counties. While standing at the entry of a 2,000 acre grassland, discussing site selection and experimental design, the manager stated, “We don’t have any prairies.” After some discussion, it became clear that there was a need to distinguish between remnant (native) prairies, and prairies that were recently converted from farmland. In this context, prairie remnant refers to a site that, according to all available land use history data, has never been farmed, heavily grazed, or converted from a prairie plant community. Some of these sites may have been subjected to light, occasional cattle grazing prior to the 1950s as well as periodic influxes of non-native vegetation, but were never subjected to substantial soil disturbance.

Prairie restoration – Sites that are classified as prairie restorations are sites that were historically prairies that were converted to row-crop agriculture and then converted back to prairie or, as is the case of unmanaged prairie restorations, has been left fallow. The duration and intensity of farming practice are frequently not available for each site. However, all of the sites were subjected to some degree of soil tillage, rotation of monospecific crops (e.g., corn, soy), and regular applications of herbicide and fertilizers.

Early management – Early management sites are those that have been restored and managed within the last 10 years. In woodlands and prairie remnants, this period coincides with the initial removal of invasive shrubs, selective herbicide application, and the reintroduction of prescribed burning. Occasionally, this also includes the addition of native herbaceous species through seeding and even less frequently, plugs. In prairie restoration, early sites have been seeded with native species either through hand broadcast or drill seeding methods in conjunction with mowing and/or prescribed burning. It is expected that, over time, some sites that were initially classified as “degraded, unmanaged, controls” will eventually move into this category. These sites are most useful for investigating questions on the more immediate impacts of restoration practices, which are often most substantial in the first few years, on key organisms and ecological processes. However, new sites may need to be added to the program over time in order to maintain this category as these sites move from the “early” to “intermediate” category.

Intermediate management – Intermediate sites are those that have been subject to restoration and management efforts for at least a decade. Over time, this category is expected to become the largest as early management sites continue to be managed and become reclassified as intermediate.

Reference – Reference sites were selected by land managers as representing what they interpret to be high quality ecosystems that represent theoretical ecological restoration targets. This quality is usually defined by plant community composition, but is not typically quantified or universal for all land managers. The definition of a “high quality” or reference site was intentionally vague when communicating site selection with land owners in order to reflect the quality interpretations of land managers and not of the researchers. These sites are managed by prescribed fire, invasive species removal, and periodic monitoring, but rarely include the reintroduction of additional plants.

Unique – The “unique” category of management exists to ensure that the program includes sites that are of particular interest to land managers but do not easily fit within the descriptors of the other categories. For example, one of the unique woodlands is currently unmanaged, does not contain a structurally or biologically diverse plant community, and is surrounded by the invasive shrub *Rhamnus cathartica*, but is not itself invaded. From the land manager’s perspective, this site should either be highly invaded, based on similar patterns of vegetation in other sites, or highly diverse, since biologically diverse sites tend to be more resistant to high densities of invasive plant species (Naeem et al. 2000, Kennedy et al. 2002). Because it is neither biologically diverse nor invaded, this site does not fit the general trend as demonstrated in the literature. As a result, some of its unique qualities might lead to a better understand of intrinsic factors that influence invasion resistance and invasion dynamics.

Application of CWLMRP in Dissertation

In chapter 2, I use this established network to address fundamental plant-soil interaction questions, examining how restoration and management activities influence plant community composition and soil nutrient availability in grasslands and woodlands. In chapter 3, I use geospatial analysis of above and belowground ecological variables to describe woodland degradation across the region and develop a model to prioritize future restoration efforts. In chapter 4, I use this framework to investigate relationships between land use history, management duration, plant communities, leaf litter decomposition, and the function and diversity of decomposing fungal communities in prairie restorations and remnants. In the final chapter, I present the results of a field study that integrates the use of soil carbon amendments and different seed mixes during the restoration of an exotic shrub dominated grassland.

I conclude my dissertation by synthesizing my findings and discussing the utility of integrating a soils perspective into restoration and land management, both before restoration begins and throughout land management. As a first step, I discuss the importance of baseline data in understanding belowground conditions, determining appropriate methods for restoration and prioritizing sites for restoration. Then, I place my findings within the context of the efficacy of ecological restoration efforts in restoring ecosystem function. Next, I investigate targeted solutions to modified belowground processes that feedback to influence aboveground communities. Throughout this dissertation, I examine the efficacy of current and historic land management activities to determine if conservation goals are being met. I also seek to provide insight into areas where actions should be sustained, directed, or redirected to meet stated regional conservation goals. Finally, I discuss how the work satisfies the professional needs of both researchers and practitioners. This integration will ultimately contribute to improved ecological framework by ensuring that urban ecosystems are included in ecological studies and that their contribution to global biodiversity conservation is documented.

Chapter 2

Impacts of restoration and management duration on above and belowground processes

Abstract

Ecological restoration efforts focus on the establishment of a biologically diverse native plant community while reinstating the ecological processes that sustain that community. The efficacy of these restoration efforts is not well-documented at the landscape scale or in an urban context. In the natural areas of the Chicago Wilderness region, restoration success may be hindered by altered plant-soil interactions as a result of fragmentation, land-use change, species invasion, alteration of nutrient cycles, lack of natural disturbances, or combinations of these factors. It is also unclear how restoration impacts above- and belowground relationships. In this chapter, I examine the impact of duration of aboveground focused restoration and ongoing land management activities on plant community composition and soil nutrient availability across 121 woodland and prairie ecosystems in a replicated restoration chronosequence in the Chicago region. I found that restoration activities generally reduced invasive species cover in favor of native species and placed plant communities on a trajectory towards reference conditions in both woodland and prairie ecosystems. In woodlands, the plant community structure of managed sites was similar regardless of management duration compared to unmanaged sites, thereby indicating that the initial action of removing woody invasive taxa is critical to initiating community recovery. However, there was minimal similarity between managed and reference sites, suggesting that restoring high biodiversity in woodlands may require novel approaches. In

contrast, prairie remnants and former-agricultural prairie restorations had distinct plant communities, supporting the application of different ecological goals and management techniques currently employed by land managers. Only soil phosphorus (P) was influenced significantly by land-use history with nearly three times as much soil P available in former agricultural sites than in prairie remnants. This result likely reflects the legacy effects of agriculture and further supports the ecological distinction between these two grassland ecosystems. No other soil variable differed by land-use history or management duration. However, total nitrogen (N) and carbon (C) and certain micronutrients (Fe, Mn, and S) were correlated with grassland plant community composition across all sites. In both remnants and restorations, plant communities shifted from non-native to native species dominated with increasing management duration. I conclude that, in prairies, land use history is the most important factor in determining plant community assemblage followed by more recent land management activities. Prior to initiating restoration, an initial site assessment should include plant community and soil nutrient analysis to determine appropriate plant community composition targets and potential challenges to reaching these targets.

Introduction

Natural areas are increasingly influenced by a wide suite of anthropogenic disturbances that may lead to a reduction in biodiversity and degradation of ecosystem composition, function, and services. As a result, these areas must be restored and/or managed to maintain conservation goals of preserving local biodiversity and function (Prach and Hobbs 2008). Within this context, ecological restoration seeks to restore a community to a target condition, often referring to a suite of species and processes present prior to significant disturbance. In the US, the referenced time period is often pre-European settlement, although variations and more recent time periods, such as prior to a significant disturbance (eg., farming) may be used (Thorpe and Stanley 2011). Other objectives include maximizing biodiversity, providing habitat for rare species, and/or rehabilitating ecosystem processes and services (Blumenthal et al. 2003; Hobbs 2007). While considerable effort has been made to examine restoration quality in the aboveground community, there has been less emphasis on the belowground processes (Heneghan et al. 2008a). In this chapter, I examine the impact of duration of aboveground-focused restoration and ongoing land management activities on plant community structure and composition and soil nutrient availability in woodland and prairie ecosystems across a restoration chronosequence in the Chicago region.

Despite best intentions, restoration efforts may be partially successful or produce unexpected or negative results (Prach and Hobbs 2008). A variety of factors can contribute to this outcome, such as land use history legacies (Kulmatiski et al. 2006), environmental heterogeneity (Baer et al. 2005, Kumar et al. 2006, Jiménez et al. 2012), anthropogenic nitrogen (N) deposition, persistence of empty niches (Levine and D'Antonio 1999), and interactions between natural and anthropogenic factors (Blumenthal 2005). An additional factor contributing to restoration outcomes is the belowground ecosystem (Harris 2003) and its processes (Perring et al. 2015). This system is frequently overlooked by restoration practitioners and conservationists alike, even though it is critical to plant community dynamics and long-term sustainability of the ecosystem (Baer et al. 2004, Heneghan et al. 2008a, Liao et al. 2008). Increasing evidence has shown that belowground ecosystem processes can be impacted by physical disturbance (Elliott 1986), atmospheric deposition (Berg and Matzner 1997, Vitousek et al. 1997, Lovett et al. 2000, Knorr et al. 2005, Phoenix et al. 2006), and plant and animal introduction (Blumenthal 2005, Knight et al. 2007, Chengzhang et al. 2008, Eisenhauer et al. 2011). As a result, these shifts in belowground ecosystem structure and function could feed back to influence the aboveground community and hinder the success of meeting many restoration goals.

In practice, restoration largely involves the aboveground removal of exotic species, the reintroduction of native species, and the reestablishment of natural disturbances, especially fire in the Midwestern U.S (Jordan 1997). These aboveground approaches are employed because they can be readily applied by practitioners and provide the most viable method of establishing a biologically diverse, native plant community. The diversity and composition of the restored plant community is often used as a measure of successful restoration. This is because diversity is generally expected to co-vary with ecosystem function (Naeem et al. 1994, Tilman et al. 1997, Yin et al. 2000, Loreau et al. 2001). However, even in remnant communities, the establishment of a diverse plant community may not necessarily correspond to increasing ecosystem function, as some species may have a more significant influence on function (Lyons and Schwartz 2001, Mouillot et al. 2013) or other measures of diversity. For example, as functional diversity may be more important than species composition (Chapin et al. 1997, Díaz and Cabido 2001) on some ecosystem processes due to functional redundancy (Walker et al. 1999). Similar studies in restored, managed or urban sites are largely lacking and most studies occur on an experimental plot rather than landscape scale. Thus, generalizations about the relationship between plant community structure and ecosystem function is difficult (Niemelä 2014, Andersson et al. 2015, Groffman et al. 2017, Lepczyk et al. 2017).

Restoration has become increasingly important in urban and suburban areas where the boundaries between human developments and protected natural areas are blurred. In addition, natural areas in urban environments are also often fragmented, subject to N deposition, exotic species introductions, and other natural and anthropogenic disturbances such as light and sound pollution (Botkin and Beveridge 1997, Grimm et al. 2008, McKinney 2008, Seto et al. 2011). In these areas, ecological restoration is seen as a way to reverse degradation and enhance or return these natural areas to a something resembling or functioning as a biologically diverse, native ecosystem. Frequently, these restoration goals are not well defined, but are roughly interpreted as achieving a particular process, suite of processes, and/or desired community composition (Hobbs 2007, Miller and Hobbs 2007, Lindenmayer et al. 2008, Thorpe and Stanley 2011).

The Chicago metropolitan region is an ideal location to investigate issues of fragmentation, disturbance, plant invasion, and subsequent restoration. The region has a long history of ecological restoration, thereby allowing for a landscape scale exploration of the effects of restoration activities on plant community composition and belowground ecological processes. The region also contains globally rare ecosystems in a heterogeneous matrix of woodland, oak savanna, tallgrass prairie, wetland, farmland, urban, and industrial land use (Heneghan et al.

2012). Despite the variability of training, employment, and authority among restoration practitioners in local municipalities, private restoration contractors, and volunteers, the Chicago Wilderness region land managers have developed a suite of best management practices for ecosystem restoration. This similarity of approach allows for a landscape scale, replicated natural experiment to address questions on how the aboveground management practices influence plant community composition and belowground processes. This landscape also capitalizes on the restoration history of natural areas across the region in a tradition that is well documented in ecological history. Further, the diverse landscape context of this restoration experiment permits the inclusion of spatially relevant ecological questions.

In this chapter, I use the restoration chronosequence described in Chapter 1 to investigate the impacts of aboveground focused management practices in woodlands and prairies on functional plant community assemblages, soil processes, and their relationships. My objective is to determine the extent to which the duration of land management influences plant community structure and soil nutrient availability in woodlands and prairies, and identify the environmental correlates of plant community composition.

Methods

Study Sites

The study sites (N = 121) represent a space-for-time experimental design in which woodland, savanna, and prairie habitats occur along a gradient of restoration or management duration. These sites are dispersed throughout the four counties (Cook, Lake, DuPage, and McHenry) of the Chicago region. Each site represents a separate management unit, though several management units may be present in a single preserve. Sites are identified by habitat as well as management category. Habitat categories include woodland, prairie restoration, and prairie remnant. Woodlands sites are defined as having approximately 25-50% canopy cover. Prairie remnants are defined as sites with no record of significant grazing, farming, or another major disturbance. Prairie restorations are former agricultural sites that are either fallow (e.g., old fields) or have recently been converted back to tall grass prairies through active restoration and management strategies that include herbicide, seeding, mowing, and/or fire. Sites are also identified by their management category. Land managers identified each included site as being representative of one of four management categories: 1) unmanaged/control; 2) recently restored (< 10 years ago); 3) intermediate restorations (restored and managed for at least 10 years); and 4) reference.

Vegetation Structure

Vegetation analysis was conducted using a modified Whittaker plot method (Chapter 1). Trees greater than 2.54 cm diameter within nine 100m^2 circles were identified to genus and species where possible and the diameter at breast height (DBH) was measured. Shrubs within nine 4-m^2 quadrats were identified to genus and species where possible and counted by height class (0.5-1.0 m, 1.0-1.4 m and >1.4 m). Vegetation cover was estimated using the Braun-Blanquet classification system in nine 4-m^2 quadrats using functional plant groups in both woodlands and prairies. In prairies, species that accounted for greater than five percent of cover per plot were identified to genus or species and their cover class was recorded as well. This method of collecting plant data into cover classes resulted in a consistent evaluation of plant cover by multiple observers across the growing season. However, this approach also presents challenges to summarizing and analyzing data and using the appropriate statistical techniques. I therefore summarized vegetation cover data in woodlands (Table 1) and grasslands (Table 2) to show the average and standard error, as well as the median and mode of each functional group by cover class.

In woodlands, canopy openness, a measurement of canopy structure and a proxy for light availability, was determined using five fisheye photographs taken at breast height and at ground level at five of the nine vegetation plots (center and each of the four cardinal directions). Images were analyzed using Gap Light Analyzer 2.0 software (Chapter 1).

Soil Characteristics

Replicate soil cores measuring approximately 7-cm in diameter and 10-cm deep were collected from each site approximately 10-m away from the center point. Soil samples were kept cool, and transported to the lab to determine moisture, pH, texture (particle size) as well as total carbon (C) and nitrogen (N). Laboratory procedures for this analysis follow the standard methods used in the United States Long Term Ecological Research (U.S. LTER) Network (Robertson et al. 1999). Soil nutrient availability was determined using commercially available ion exchange membranes (Plant Root Simulator^{TM}, hereafter, PRS^{TM} probes) (Johnson et al. 2007). PRS^{TM} probes were then analyzed for macronutrients, ammonium (NH_4^+), nitrate (NO_3^-), phosphate ($H_2PO_4^-$, HPO_4^{2}), potassium (K^+), calcium (Ca^{2+}), magnesium (Mg^{2+}), sulfate (SO_4^{2-}), and micronutrients, Iron (Fe^{2-}), aluminum (Al^{3+}), manganese (Mn^{2+}), copper (Cu^{2+}), zinc (Zn^{2+}), boron (B^3+), and lead (Pb^{2+}) as µg nutrient per cm^2 over 28 days during the peak growing season in 2009-2012.

Statistical analysis

Vegetation data is summarized by management category for woodlands and by management category and land-use history for prairies using the average, standard error, median, and mode cover class for each vegetation functional group (Table 1 and 2). All analyses were conducted using the R-studio interface to R (2015). Differences in plant community composition among sites was calculated and visualized with non-metric multidimensional scaling (NMDS) using the *vegan* package (Oksanen et al. 2015). Bray-Curtis dissimilarity distances were calculated from the median cover class in each functional plant group. Woodland cover-class data was square root transformed prior to ordination to lower stress. Transformations on prairie cover data did not influence ordination stress and were not performed.

Permanova with 10,000 permutations was used to determine if there were significant differences in plant community structure with respect to management category, county, and interactions between these variables. Analyses for prairie sites also included land-use history (remnant or restoration) as an explanatory variable. Correlations between plant communities and soil physical and chemical factors were analyzed using *envfit* with 10,000 permutations, where significant differences were defined as $p < 0.05$ and are plotted on the ordination figures with their corresponding vectors.

The non-parametric Kruskal-Wallis test and Analysis of Variance (ANOVA) were used to determine if there were significant differences in soil physical and chemical variables between management category (woodlands, prairies) or land-use history (prairies). For significant variables a Dunn post-hoc test was used to determine differences among management categories.

Results

Woodland Plant Community Structure

Woodland plant community structure differed significantly between management categories (Figure 1; $R^2 = 0.097$, $p = 0.004$), with unmanaged sites differing significantly from managed/ remnant sites. Canopy openness ($R^2 = 0.24$, $p = 0.005$) and soil Ca ($R^2 = 0.19$, $p = 0.013$) and B ($R^2 = 0.28$, $p = 0.002$) were significant explanatory variables of plant community composition. Axis 1 represents an increase in canopy openness and soil B levels, whereby canopy openness and soil B are higher in managed than unmanaged sites (Table 3). Community differences among managed and reference sites were best explained by soil Ca levels (Axis 2,) with lower soil Ca levels in reference than managed sites (Table 3).

Canopy Openness

Canopy openness significantly differed among management categories ($\chi^2 = 12.89$, $p = 0.0049$; Figure 2,) where control sites have the least canopy openness and intermediate are the most open. Post-hoc pairwise comparisons show that the difference between control and early sites is approaching significance ($p = 0.052$) and the only significant difference is between the control and intermediate management categories ($p = 0.006$).

Prairie Plant Community Structure

Plant community structure for all prairie sites differed significantly by land use history ($R^2 = 0.06$, $p < 0.001$; Figure 3). Prairie restorations were associated with non-native grass and forb cover. Remnants were associated with woody stem, sedge and rush, and moss cover. Plant community structure also differed significantly in response to management duration ($R^2 = 0.108$, $p < 0.001$) and county ($R^2 = 0.10$, $p < 0.001$; see Appendix) with significant interactions detected between management duration and land use history ($R^2 = 0.056$, $p < 0.001$). None of the environmental variables tested explained the variation in plant community structure. Because of this clear distinction in plant community structure by land use history, all further comparisons of plant communities were separated into prairie remnants and prairie restorations.

Prairie remnant plant community structure significantly differed by management duration ($R^2 = 0.14$, $p = 0.001$) and county ($R^2 = 0.17$, $p = 0.03$; Figure 5). Soil available NH_4 ($R^2 = 0.33$, $p = 0.02$), Al ($R^2 = 0.31$, $p = 0.03$), and total C ($R^2 = 0.32$, $p = 0.03$) was correlated with plant community structure but not management duration (Table 4). Available NH_4 and Al were correlated with non-native forb cover and total C was correlated with non-native grasses, sedges and rushes, and detritus.

Prairie restoration plant community structure was significantly different among management duration category ($R^2 = 0.22$, $p < 0.001$; Figure 6). Unmanaged sites were associated with increasing levels of non-native grass cover while early management sites had the greatest cover by non-native forbs and woody stem cover than other sites. Intermediate and reference sites were similar to each other and associated with native grasses and forbs. Intermediate sites had greater dissimilarity within the category than reference sites. The wider spread was influenced by three sites that were more similar to early restoration sites in that they had higher non-native grass and forb cover, moss, and bareground. No environmental variables were significantly correlated with plant community structure, although there were modest correlations with NO_3 ($R^2 = 0.14$, $p = 0.052$) and total inorganic N ($R^2 =0.14$, $p = 0.54$), mostly driven by NO_3 and correlated with non-native forb cover.

Prairie Soil Nutrient Availability

Of all the soil factors tested, only soil P availability differed among site categories. Land-use history significantly influenced soil P ($F = 13.967$, $p < 0.001$, Figure 3) with almost three times more P in soil from former agricultural prairie restorations than prairie remnants. All other soil variables were similar between land use histories and land management category (Table 4).

Discussion

Using a network of 121 woodland and prairie sites, I examined and systematically documented, for the first time, a regional perspective of terrestrial restoration and management. Through this replicated, landscape-scale approach, I found that restoration and on-going management successfully reduced invasive species and increased native species cover in both woodlands and prairies.

The return of a plant community to a similar structure and composition to a reference ecosystem is often the measure of success for an ecological restoration (Martin et al. 2005, Ruiz-Jaén and Aide 2005, Ruiz-Jaen and Mitchell Aide 2005). However, there is considerable critique of this method of evaluation since the restoration of vegetative composition or structure does not necessarily indicate the restoration of ecological processes (Ruiz-Jaén and Aide 2005, Cortina et al. 2006, Benayas et al. 2009). My results indicate that at a landscape scale, restoration efforts successfully place plant communities and processes on a trajectory that aligns with conservation goals and provides a link between management practices and above- and belowground processes.

While my results are similar to other management chronosequence studies that demonstrate the establishment of a vegetation matrix toward that of the original ecosystem with increased time under managment (Baer et al. 2002, Hansen and Gibson 2014), my study differs by showing that the links between plant community composition and nutrient availability are unique compared to other studies (Kulmatiski et al. 2006, Kettenring and Adams 2011). The soil nutrients that correlate to plant community structure differed between woodland and prairie systems and differ from other studies. I therefore suggest that the underlying mechanisms that link soil fertility and plant community structure are context-specific and cannot be generalized throughout a large region, but likely influence restoration outcomes. As a result, soil nutrient availability should be more thoroughly explored prior to and throughout management in order to more accurately define and meet restoration goals.

My results indicate that throughout the Chicago Wilderness region, restoration and ongoing management result in plant communities that meet conservation goals of reducing invasive species dominance in favor of native species. The positive impacts of restoration efforts were more visible in woodlands, where the physical removal of invasive shrubs results in an immediate and highly visible change in plant community structure toward a reference woodland. In prairies, however, long-term land use legacies of farming appear to supersede more recent land management impacts on plant communities. I discuss each of these in turn.

Woodlands

Above and belowground outcomes of woodland restoration in the Chicago region suggest that aboveground focused restoration activities successfully reduce invasive shrub dominance in favor of native plant cover. These initial results provide further impetus for the region’s volunteers and land managers to initiate restoration at unmanaged or degraded sites. Simply beginning the ecological restoration process by removing invasive species is a critical step in the right direction.

The clear separation of the unmanaged sites from all of the other managed sites, regardless of management duration, indicates that simply initiating aboveground restoration at a site puts it on a trajectory towards target plant community composition. This interpretation is further supported by other analyses that demonstrate that managed woodlands, regardless of time since restoration have significantly lower invasive shrub cover, soil available nitrogen, and earthworms (Chapter 3), all variables that are linked to woodland degradation (Bohlen et al. 2004, Eisenhauer et al. 2011). The lack of clustering of managed and reference sites also suggests that while general practices are similar and well replicated throughout the region, nuances in specific manager approach, site conditions, land use history, and ecological context might have significant impacts on biodiversity outcomes, regardless of duration of restoration and management. Rather than view this outcome as a lack of regional trend toward a reference condition, this beta-diversity, on a landscape scale, might contribute to biodiversity conservation on a regional scale.

The slight overlap, but otherwise distinct differences in plant communities of reference sites and all other managed sites, including those that have been managed for decades, suggests that duration of management is not enough for woodlands to reach reference conditions. This could also indicate that there is something inherently unique about reference sites and/or that these sites might not be appropriate references for other managed woodlands. With this in mind, I suggest that the land management community re-evaluate the utility of selecting certain sites as reference or theoretical restoration targets. Instead, I suggest that managers describe site- or habitat-specific goals for restoration that target a specific assemblage of species, a target diversity, or a community that is sustained with minimal further intervention. This notion is supported by others particularly where either reference sites don’t exist or are inappropriate considering landscape-scale alterations of connectivity, specifies composition and disturbances (White and Walker 1997, Choi 2004).

Prairies

Historical agricultural use was the most significant factor influencing plant community composition in prairies. Prairie restorations were characterized by non-native grasses and forbs while prairie remnants had higher woody stems and sedges and rushes. Soil legacy impacts likely influence this difference as former agricultural prairies that were restored had more than three times the amount of available phosphorus than prairie remnants. This result supports the application of different ecological goals and management techniques currently employed by land managers given historical land use (Rowe 2010). I anticipated a distinct plant community composition between these two prairie habitats during the experimental design and site selection process when I initially considered including all grasslands in one habitat category. A land manager in McHenry county pointed out this experimental design flaw very early in process by stating, “We don’t really have any prairies. We have lots of restorations,” indicating a clear difference in restoration and management approach between the two types of grassland habitats (Ed Collins, personal communication). In this study, I documented the distinction between remnants and restorations in both the plant community and soil characteristics.

Despite the challenges associated with restoring a former agricultural site to native prairie, management efforts significantly impact plant community composition, showing a clear trajectory from non-native to native species dominance. Prairie restoration success is indicated by the trajectory across axis 1 where old fields (control) are more associated with non-native grasses, and references are more associated with native grasses. Early and intermediate sites serve as a transitional phase, with sites distributed across a wider range and more characterized by woody stems, bareground, native forbs, and detritus. Differences in plant community composition among prairie remnants were driven by land management duration and county, but sites were more tightly clustered within than among prairie restorations.

Plant communities for all unmanaged and reference sites are closely clustered for each habitat type, suggesting that these two categories are relatively well-defined and similar across the landscape. Wide dispersal plant communities for early managed ecosystems, which narrows with intermediate management, supports the hypotheses of reassembly following major disturbances (Drake 1990, Hobbs et al. 2007).

Management activities do not have the same impacts on soil processes as plant communities and none of the measured soil nutrients measured were correlated with plant community composition. This lack of a clear relationship suggests that both historical and modern land-management activities are a more significant driver of plant community composition than above- and belowground interactions. Thus, management activities and ecological goals can remain generalized on a regional scale, but will likely be most successful while still accounting for unique local conditions.

Further Investigation

An important result of my study is that time under restoration is not an inclusive metric of management efforts. While it would be reasonable to expect that a system that is managed for an extended period of time would result in higher quality (biodiversity) ecosystems, time is not the only factor that should be considered when quantifying the management activity. Other factors include site context at a preserve and landscape scale, long-term land use history, and the initial condition prior to restoration.

For future studies, management intensity may be a more accurate metric than management duration. However, determining an appropriate way to document and quantify management intensity is challenging, as data is often unavailable since specific actions are often reactionary and not always documented. Measures of management intensity could include the number of visits, activity hours, dollars per acre, equipment used (manual or power tools), seed application, presence, absence or frequency of fire, expertise of restoration leader, etc. While these variables are difficult and occasionally impossible to collect, and therefore not included in this program, their role in determining plant community assemblage should still be acknowledged.

Finally, a long-term perspective is critical to developing our understanding of a broad suite of ecological phenomena and processes. Documenting and forecasting ecological change, particularly in relation to active land management, also requires an understanding of interactions of spatial and temporal dynamics of ecological systems, necessitating studies at multiple spatial scales (Kratz, 2003). The Chicago region has a rich history of restoring natural areas and has been internationally recognized for such coordinated, regional-scale efforts. As such, the CWLMP, like LTER sites, are intentionally and uniquely established for these investigations.

Chapter 3

Identifying restoration challenges and opportunities using spatial interpolation

Abstract

Urban and suburban woodlands are increasingly subjected to disturbances that negatively impact biodiversity and ecosystem functioning. As with woodlands worldwide, forest fragmentation, invasions by exotic plants and European earthworms, and elevated soil nitrogen (N) are major threats to woodland ecosystems in the Chicago region. These threats frequently co-vary and their combined negative impact poses a greater threat to woodland biodiversity and system functioning than any single factor. A major challenge has been to identify the spatial distribution of these co-varying threats in ways that could be used to prioritize restoration and land management efforts. Here, I address this challenge by analyzing woodlands along a restoration chronosequence, a space-for-time substitution that includes both unmanaged sites and sites that have been restored and managed for varying numbers of years. First, I examined the separate effects of management duration on soil N availability, earthworm biomass, and exotic-shrub densities. Then, I applied geospatial techniques using these threat variables to develop a predictive spatial model of woodland degradation, thus creating a predictive restoration challenge index. Land management significantly reduced all three threat variables compared to unmanaged sites, suggesting that aboveground focused woodland management efforts can impact both above- and belowground ecological threats. Spatial interpolation of all three variables was used to a create restoration challenge index across the entire study area. This

indicated that most unmanaged sites conformed to the trend of being high woodland restoration challenges. As a result, managers could continue to use observed levels of invasive shrub dominance as a predictive tool for determining the severity of earthworm invasion and soil N availability prior to beginning restoration efforts as a predictive tool. Notably, some unmanaged areas were low on the woodland restoration challenge index, with lower levels of one or more of the three measured threats. It is possible that these latter sites may have a higher probability of restoration success. In those areas, I encourage managers to investigate current levels of exotic earthworm invasion and soil N availability prior to beginning restoration efforts to validate this prediction and facilitate more cost-effective restoration. By integrating traditional ecological data with spatial modeling, my study illustrates how to move beyond simply explaining impacts of restoration on individual ecological processes to using a spatially-explicit sampling of a few targeted variables to reveal both ecological hurdles to management efforts and where opportunities for successful restoration outcomes might exist across the landscape.

Introduction

Invasive species are recognized as a major threat to biodiversity, second only to habitat destruction (Wilson 1999, Shochat et al. 2010). Studies suggest that soil disturbances and high levels of soil fertility may enhance non-native plant invasions (Ehrenfeld and Scott 2001, Ehrenfeld 2003, Suding et al. 2004, Kulmatiski et al. 2006, Chengzhang et al. 2008, Pieri et al. 2010, Weidenhamer and Callaway 2010), and that feedbacks between above- and belowground systems may have multiplicative negative impacts on biodiversity and ecosystem function in invaded systems (MacDougall and Turkington 2005, Knight et al. 2007, Eisenhauer et al. 2011). Unfortunately, non-native species are also becoming increasingly abundant in urban areas (Blumenthal 2005). These protected, but highly fragmented natural areas are also subject to anthropogenic nitrogen (N) deposition (Vitousek et al. 1997, Lovett et al. 2000, Kaye et al. 2006, Grimm et al. 2008), which may further facilitate the spread of invasive species (Ross et al. 2011) and reduce native species diversity and abundance (Vilà et al. 2011). However, the inter-relationship between soil N and invasive plants is not well understood (MacDougall and Turkington 2005, Bauer 2012). In this study, I examined the separate effects of management duration on exotic-shrub densities, earthworm abundance, and soil N availability, and applied geospatial techniques to develop a predictive spatial model of woodland degradation and thus create a predictive restoration challenge index.

In the Midwest United States, *Rhamnus cathartica* (European buckthorn, hereafter, buckthorn) is a problematic invader of woodlands and prairies. Research shows that buckthorn invasion is associated with elevated soil N and increased biomass and abundance of exotic earthworms (Heneghan et al. 2007b, Knight et al. 2007) that, together, are detrimental to woodland biodiversity and ecosystem functioning of natural areas (Noss 2000, Heneghan et al. 2008b). However, the precise mechanisms and feedback relationships between these factors is unclear (Iannone et al. 2015) and the impacts of aboveground focused restoration efforts on belowground processes are not well understood (Madritch and Lindroth 2009, McCary et al. 2015). Further, there is still no tool to predict if observed correlations with earthworms and soil N exist throughout buckthorn's range, or if there are other factors that may influence restoration efficacy. Because of the prevalence of this invader and the known impacts of shrub invasion on biodiversity conservation in the region, buckthorn is actively removed from protected sites with the goal of restoring native plant diversity and ultimately ecosystem function.

A spatial perspective is critical for conservation planning, modeling biodiversity outcomes, and contextualizing ecosystems into the human landscape (Suter Ii 2001, Fraser et al. 2009). However, use of geospatial tools is not common and often not necessary in replicated laboratory and field studies where response variables can be compared using single or multivariate statistical models (Dale and Beyeler 2001, Gazol and Ibáñez 2009). Recent advances in geospatial technology have the potential to illuminate patterns and processes observed in ecological studies that may otherwise not be apparent.

In this study, I investigated the impacts of restoration duration on exotic earthworm biomass, soil N availability, and invasive shrub cover using traditional ecological and geospatial techniques. Using a restoration chronosequence of woodlands in the Chicago region (Chapter 1), I examine the effectiveness of current restoration and land management practices on reducing these three ecological variables to: 1. Determine the impact of restoration on key aboveground (invasive shrub cover) and belowground (earthworm biomass and soil N availability) properties;

and 2. Generate a spatially explicit model of woodland degradation that can serve as a restoration challenge index and potentially guide future restoration efforts. This study will describe, on a landscape scale, the impacts of current aboveground focused management efforts on restoring ecological processes and offer practical, location-specific approaches to prioritizing restoration efforts. I chose this two-pronged approach because patterns that appear obvious using conventional ecological community metrics can become blurred when investigating them on a larger spatial scale, and vice-versa.

Materials & Methods

Study Sites

This study was undertaken at 44 woodlands that are a part of the Chicago Wilderness Land Management Research Program, known colloquially as “100 Sites for 100 Years” (Heneghan et al. 2012). Each site represents a separate management unit, though several management units may be present in a single preserve. Study sites were selected by land managers along a gradient of restoration or management duration throughout four counties (Cook, Lake, DuPage, and McHenry) in the Chicago region. Sites were identified as being representative of one of four management categories (Table 3). Unmanaged or degraded sites in this region are those that have not been restored or managed in recent history and can be best described as a dense thicket of invasive shrubs dominated by European buckthorn (n = 12). These sites serve as a control. Recently restored sites were once dense shrub thickets that were restored within the last ten years through cutting woody stems and applying herbicide to cut stumps, and have been continually managed using adaptive management strategies following initial buckthorn removal (n = 13).

Intermediate restorations are similar to recently restored sites, but active management has occurred on those sites for at least 10 years (n = 12). Reference sites refer to those that are considered high-quality, biologically diverse woodlands that were selected by land managers and serve as their theoretical restoration targets. They do not have any recent history of significant exotic shrub invasion and are actively managed.

Soil Nitrogen Fertility

Soil nitrogen availability was measured using Plant Root Simulator Probes (hereafter PRS^{TM} probes) from Western Ag Innovations (http://www.westernag.ca/innov/index.php) (detailed in Chapter 1). In 2009 and 2010, two replicate sets of cation and anion PRS^{TM} probes were inserted vertically into the soil to a depth of 10 cm for 28 days, removed, cleaned and then analyzed by Western Ag. Innovations. In each site, soil N fertility represents the sum of the inorganic µg nitrate (NO_3^-) and ammonium (NH_4^+) per cm^2 soil over 28 days.

Earthworm Abundance

Earthworms were sampled at 15 of the 44 woodland sites from four replicate 0.25m^2 square areas located ten meters to the north, south, east, and west of the central point of the plot. Earthworms were extracted from the soil using a slurry of 38.1 g of ground oriental mustard in 5 L of tap water (Gunn 1992, Lawrence and Bowers 2002, Iannone III et al. 2012). Sampling occurred before 12:00 pm from 21 to 29 June 2010 to avoid peak temperatures, which may affect sampling (Institute 2011). Collected earthworms were transported to the lab in sealed containers with a moist paper towel in a cooler. Adults were then identified to species (for all *Lumbricus spp.*) or genus. Juvenile earthworms were identified as *Lumbricus* spp. juveniles or nonpigmented endogeic juveniles. All earthworms were counted, allowed to vacate their gut contents in a refrigerator for 48 hours, and were then dried for 48 hours at 60°C and weighed to determine their dry biomass (Institute 2011).

Measures of Woody Plant Invasion

Invasive woody shrub cover was estimated visually at every site using the Braun-Blanquet ordinal cover classification system as described in Chapter 1 (Braun-Blanquet 1932). All vegetation sampling was conducted during the growing season (mid-June to late-August) between 2009 and 2011. The midpoint of each was then averaged to determine a mean percent cover of invasive shrubs at each site. Mean invasive shrub cover for each management category was then calculated from calculated average site cover.

Data Analysis

Replicate samples for total soil inorganic N ($NO_3^- + NH_4^+$), total earthworm biomass, and invasive woody shrub cover were averaged for each site and management category. Statistical models were selected through backwards elimination. Soil N and vegetation were modeled with management type, year, and management type by year interactions as explanatory variables. Targeted pairwise comparisons were then made between control and managed sites, and between management categories when significant differences within management type was observed. All data were analyzed using R studio (2015).

GIS Methods

Spatial analysis was conducted with ArcMap10 (ESRI, 2012) using GCS North American 1983 projection. Illinois state county boundary shape files were obtained from the Illinois Natural Resources Geospatial Data Clearing House (http://crystal.isgs.uiuc.edu/nsdihome). Each study site is represented by a tree canopy outline and the corresponding management category is displayed using a red to green color scale where red indicates unmanaged, orange indicates recently restored (< 10 years), yellow indicates intermediate management (> 10 years), and green indicates that the manager has designated the site as a reference woodland. Blue symbols represent sites that do not fit one of these management categories (referred to as "unique" in Chapter 1) and were not used in univariate analysis, but were used in spatial interpolation to provide additional spatial coverage.

Individual raster layers were created from averaged soil nitrogen availability, total earthworm biomass, and invasive shrub cover using the "Inverse Distance Weighting Squared" (hereafter, IDW^2). This spatial interpolation tool assumes that variables of sites that are closer to one another are more alike than those that are further apart. Therefore, IDW tool estimates values for unknown points based on the values from sampled values. Closer points have more influence than those further away and values are calculated as the inverse distance weight squared. This method is preferred over other spatial interpolation tools such as diffuse interpolation, global polynomial, kernel, or kriging because there are minimal assumptions about the data input and the general approach is appropriate for environmental variables (Gambolati and Volpi 1979). All interpolations were conducted to the rectangular extent of the four studied county boundaries with a power of two, making the IDW^2 inverse distance square weighted with a full sector and minimum neighborhood of ten. Classification breaks and class number were manually adjusted so that they were most ecologically appropriate and correspond to the same scale as collection method for each degradation variable. A red to green color spectrum (high to low), was selected as a visible indicator of quality for all maps to correspond with the color coding for site management categories.

These three raster layers were then multiplied using the Map Algebra Raster Calculator tool within the Spatial Analysis toolbox to generate a raster map that is a model of regional woodland degradation or a restoration challenge index. Multiplication was selected rather than addition due to hypothesized compounding impacts of above- and belowground components that negatively impact an ecosystem (Simberloff and Von Holle 1999, Tiunov et al. 2006, Heneghan et al. 2007b, Knight et al. 2007, Nuzzo et al. 2009). This final woodland degradation raster layer was then clipped to the county boundaries in order to limit the scope of the final map to the counties included in the study and to ensure there were no indications of woodland habitat in Lake Michigan, the eastern extent of Cook and Lake Counties.

Results

Soil Fertility

Soil inorganic N availability differed significantly among management categories ($F = 3.1$, $p = 0.04$). Targeted pair-wise comparisons showed that unmanaged sites had significantly higher soil N availability than any of the managed sites ($p < 0.01$). There was no significant difference in soil N levels among managed sites ($p \geq 0.5$, Figure 2).

Earthworms

Earthworm biomass differed significantly among management categories ($F = 9.1$, $p < 0.001$). Pair-wise comparisons indicate that earthworm biomass was significantly higher in unmanaged woodlands than all other managed areas ($p < 0.05$, CI = 95%). However, there was no significant difference in earthworm biomass between other management categories ($p \geq 0.18$).

Woody Shrub Invasion

Woody shrub cover was significantly different among management categories ($F=4.4$, $p < 0.01$). Targeted pair-wise comparisons indicate that woody invasive cover was highest in the unmanaged sites compared to all other managed sites ($p<0.01$). Reference sites had the lowest invasive shrub cover, but not significantly lower than the other managed sites ($F = 2.5$, $p = 0.1$).

Modeled Woodland Degradation and Restoration Challenge Index

The raster map shows that several unmanaged sites are in areas that are high on the modeled woodland degradation index, and that most reference sites are low on this modeled index. This result corresponds with the three variables as analyzed independently. There are notable exceptions to this pattern in the northern and southern regions of the map where unmanaged sites are low on the index, though no reference sites are high on the index. Generally, sites to the east are lower on the index, while sites to further west area higher.

Discussion

I addressed the challenge of determining the impact of aboveground focused restoration on soil N availability, exotic earthworms, and invasive shrubs in urban woodlands across a restoration gradient and applied geospatial techniques to develop a predictive spatial model of woodland degradation, thus creating a predictive restoration challenge index that could be used to prioritize future restoration and land management efforts. I found that, in the Chicago Wilderness region, aboveground focused land management activities effectively reduced three key ecological threats to woodland biodiversity and ecosystem functioning, soil N, earthworms, and buckthorn cover. This finding suggests that current management practices, while operationally focused on aboveground invasive plant management, can have significant impacts on belowground variables that are implicated in reducing biodiversity and ecosystem function in invaded woodland ecosystems. This is consistent with other studies on the suggesting that aboveground management strategies can positively influence belowground processes (Kardol et al. 2007, Madritch and Lindroth 2009) but offers a different perspective to the growing literature describing the potential long-term belowground biotic and abiotic legacy effects of exotic shrub invasion (Heneghan et al. 2006, Heneghan et al. 2007b, Elgersma et al. 2011). While this information is useful alone, combining them into a spatial model provides a powerful predictive tool that has not previously existed.

Results from the ecological component of this study suggest that unmanaged sites have high soil N, earthworms biomass, and invasive shrub cover, the “trifecta” of woodland degradation. Reference sites are low in all three degradation variables. Individually, each of these were significantly reduced with management, but neither duration of management nor qualitative identification of a site as a reference ecosystem had a significant influence on any of the variables. The patterns observed for soil N availability differ from global or national models where elevated soil, primarily via atmospheric N deposition is higher in closer proximity to urban areas (Lovett et al. 2000, Kaye et al. 2006). The results of this study, based on site-specific data show the opposite pattern, where woodlands in the most urbanized county included in this study had lower, soil N levels on average, though these results were not statistically significant.

Reference sites had lower, but not statically significant, invasive shrub cover than intermediate and early management sites. This is likely due to the careful monitoring and management activities in these relatively high-profile sites where there is often “zero tolerance” for invasive species, resulting in their rapid removal. It is also possible that these sites are interpreted by land managers as reference sites specifically because of this low invasive shrub presence. However, this definition of a reference site being one with low invasive presence was never explicitly stated by the land owners/managers selecting sites. Reference sites were generally described has having a high diversity and/or quality of native plant species rather than low invasion presence.

A geospatial approach to ecological data shows that there are notable exceptions to observed patterns that may help to direct future management efforts. Prior to initiating woodland restoration at a site, earthworm and soil N availability should be measured to determine approximate levels of ecosystem degradation and the difficulty of reaching restoration goals. Sites targeted for restoration are typically those that are dominated by invasive shrubs, with little account for belowground processes that might facilitate shrub invasion or further invasive species dominance at the expense of native species (Kourtev et al. 1999, Ehrenfeld 2003, Kulmatiski et al. 2006, Knight et al. 2007, Chengzhang et al. 2008, Eisenhauer et al. 2011). Thus, sites with relatively lower levels of soil N availability (< 100 µg/cm^3/28days) and earthworm biomass (<10 g/0.25m^2) should be prioritized for restoration, as efforts there are more likely to be successful than at sites with more altered belowground components.

Given previous studies on relationships between invasive earthworms, soil fertility and invasive shrubs, a combination of these three variables could be a useful indicator of high ecological degradation (Kourtev et al. 1999, Hale et al. 2005, Heneghan et al. 2007b, Knight et al. 2007, Nuzzo et al. 2009, Eisenhauer et al. 2011). Presenting this data spatially is useful in that the variables describe three very different, but significant, above- and belowground components of terrestrial woodland ecosystems that are otherwise difficult to examine collectively due to different units of measure. The use of spatial interpolation to create a continuous surface of each variable on a regional scale allows for the generation of a predictive model for sites not included in this experiment. Combining each of these layers allows for a qualitative (rather than quantitative, since there are no scientific units to report and displayed values are relative) visual representation of degradation in the Chicago region. This combination creates a unique geospatial view of ecological factors that as they relate to current management activities and to each other. The generated woodland degradation map shows the spatial relationship of these three measures of degradation is useful in that it identifies key sites that are prime examples of the ecological patterns observed as well as exceptions to these trends.

By treating the four-county region as a continuous surface, land managers and conservation organizations could use this map to direct future land acquisitions and future direct management action. By visually representing current "hot spots" of woodland degradation within the Chicago Wilderness region, attention is brought to those areas that are potentially in need of new or increased ecological management beyond municipal boundaries. Conversely, these unmanaged areas that are highly degraded might require extensive resources in order to restore and maintain them for conservation purposes; resources which might be better directed elsewhere.

Implications for Management

Land owning agencies and ecosystem managers continue to face limited resources to implement restoration and ongoing management. This study demonstrates the ecological effectiveness of current best management practices as employed and replicated across the region and supports the conclusions of other recent studies suggesting a “Just Do It” approach to restoring woodlands (Chapter 2). These two studies investigating plant community changes with duration of land management activities and the impacts of socio-political components of land management activities on biodiversity in Chicago woodlands conclude that neither duration of nor the decision-making process associated with restoration activities impact ecological outcomes and that simply initiating restoration effectively achieves many measurable conservation outcomes.

Application of spatial analysis to key ecological variables that would have otherwise have only been analyzed using traditional approaches has broader implications as to how these observed patterns vary across a region and suggest that these general trends might over-simplify observed ecological patterns and not accurately demonstrate regional differences. This tool can also be used the determine current ecological condition of each site in relation to adjacent sites in a way that allows managers to understand the current condition of each site and potentially direct management efforts. Given the conclusions drawn from the ecological component of the study, we'd expect to see the site management categories correspond to similar background colors (e.g., red-red, green-green) showing the similar trend of management category to woodland degradation variables. While there are several areas where this pattern is present, there are some notable exceptions.

Several unmanaged sites in the northern and eastern extent of the map are in areas that are primarily green, indicating low levels of degradation. In these regions, I hypothesize that restoration outcomes will be more positive than in other areas, as they lack the compounding effects of the three indicators of woodland degradation.

Beyond directing the ongoing restoration and management activities of existing natural areas, this degradation map could also assist in the prioritization of land acquisition. For example, if land becomes available for purchase by a conservation agency in an area that is mapped as being of low degradation, this site could have high potential for conserving native biodiversity and might be a higher priority if all other social, economic, and political considerations are equal.

Given the increasing limitation of available resources for both ongoing and new restoration and management activities, the results of this study could also lead to complacency and ultimately a reduction in overall management actions with an alternative interpretation. One could justify reducing resources available for ongoing management activities at established woodlands, based on the conclusion that invasive shrub cover, soil N availability, and earthworm biomass are no different in sites that were just restored from those that have been undergoing management for several years or even decades. However, it is important to note that all categories of “managed” woodlands undergo some degree of ongoing management activities that include, but are not limited to, prescribed fire, follow-up invasive species control, and occasionally the reintroduction of native seed, all of which likely contribute to a reduction in the measured degradation variables. As helpful as this finding is for confirming the effectiveness of current restoration and land management practices, this does little to direct future restoration land management efforts, where resources are always limited.

Limitations and future research

The true test of the applicability of the model is yet to be field-tested. Anecdotal evidence confirming or disputing the model can help refine this model and direct future restoration for more cost-effective restoration of currently unmanaged and invaded woodlands. My suggestion is for land owners that are undergoing strategic planning and directing future management activities, particularly those with protected open space properties in low degradation (green) areas, to first collect baseline information on soil N availability and earthworm biomass prior to initiating a restoration program. If a given woodland is currently an unmanaged and has high invasive shrub density, but relatively soil N and earthworm biomass, I hypothesize that restoration will be successful. Conversely, I suggest that land owners in areas of high degradation prepare for ongoing challenges in the restoration process and plan resources and activities accordingly. While I’m not suggesting that these unmanaged areas continue as such, I want to emphasize the potential for greater restoration intensity and duration that might be needed at these sites in order to achieve desired ecological goals.

A valuable test of the results of this generated model would be to test the conclusions through on-the-ground restoration. The first step would be to test the accuracy of this model by sampling the soil N availability, earthworm, and invasive shrubs across a range of predicted woodland degradation values. Then, begin restoration at a several unmanaged sites across this range to determine if restoration is, in fact, more effective in areas of low degradation and more challenging in areas of high degradation

In the future, the extension of the study area to include the adjacent Kane and Will counties would improve the model. Additional sampling to in the eastern range of the study area would also improve the sampling density in that area, but is largely limited by the urban landscape, where large (≥ 1 hectare) publicly owned and managed woodlands are rare. The lack of data at the eastern extent of the study area due to the presence of Lake Michigan is the primary limitation of this analysis.

Chapter 4

Should we sweat the small stuff?

Effects of land use history and management duration on decomposition, microbial function, and diversity.

Abstract

Ecological restoration seeks to restore native organisms and the ecological processes that sustain them. While decomposition and soil biological diversity are recognized as important to ecological function and overall biodiversity, studies on the impacts of land management on this process are scarce. This study investigates the impacts of land use history and aboveground restoration practices on leaf litter decomposition, microbial function, and diversity. Mesh litterbags containing 4-10g of dried *Andropogon gerardii*, *Rudbekia subtomentosa* and *Baptisia australis*, representing commonly occurring grass, forb and legume species with differing litter qualities were secured to the soil surface of 23 study sites in March 2013. The study sites are a subset of the Chicago Wilderness Land Management Research Program (100 Sites for 100 Years) and include remnant prairies and former row-crop prairie restorations that are replicated along a restoration chronosequence. Each site, selected by land managers, exemplifies the region’s unmanaged, recent, and intermediate restorations as well high-quality reference prairies for each land use type. Plant community structure was determined by estimating functional plant group cover. Soil nutrient availability was determined using Plant Root Simulator probes. Decomposition was measured as total dry mass loss in the field as a function of time. Soil

microbial function was determined using enzyme assays and diversity through high-throughput DNA sequencing. Plant communities differ by both management and land use history and show a trajectory of increasing similarly to a reference system with longer duration of management activities. Soil phosphorus availability was more than four times greater in former row-crop prairie restorations compared to remnant prairies, but all other soil nutrients were similar across land use history and management duration. Decomposition rates differed by litter type but not land use or management history. Microbial activities were highly variable by land use, management, litter type, and enzyme substrate with no clear patterns. Functionally, there was little difference in microbial community composition, but DNA analysis indicates that species composition differs by land use history and management duration. This suggests that there is functional redundancy within the fungal decomposer community. The results of this study suggest that land use history and land management practices influence plant and fungal communities, but have little influence on decomposition and varied impacts on soil microbial activity in urbanized grasslands.

Introduction

Ecosystem restoration is a relatively young practice and efforts to restore native plant communities are sometimes met with mixed results (Prach and Hobbs 2008). One of the biggest contributors to limited restoration success is the neglect of belowground ecosystem processes (Heneghan et al. 2008). Belowground processes underpin the aboveground assemblage and contribute to the long-term sustainability of the ecosystem. By neglecting these processes, the ultimate success of meeting many restoration goals may be hindered. In practice, restoration often involves the aboveground removal of exotic species, reintroduction of native species, and reestablishment of natural disturbances such as fire. These aboveground approaches are employed primarily because they are pragmatic, and because establishing a biologically diverse, native plant community is often used as a measure of a successful restoration. However, the establishment of a target plant community alone is not necessarily equivalent to a fully functioning ecosystem and there is considerable scientific debate as to the degree to which biodiversity and ecosystem function are related (Tilman et al. 1997, Loreau et al. 2001, Johnson et al. 2007, Reza and Abdullah 2011)

Restoration is particularly important in urban areas where the boundaries between human developments and protected natural areas are blurred and where natural areas are subjected to a suite of anthropogenic disturbances that likely negatively impact long term viability of the protected space. Natural areas in urban environments are often fragmented, subjected to N deposition, species introductions, and other natural and anthropogenic disturbances (Heneghan et al. 2007a, Vačkář et al. 2012, Kandziora et al. 2013, Michez et al. 2013). Restoration is often employed to enhance or restore these natural areas to something reminiscent of their previous state, though this state is rarely described in detail. Ecologically, restoration goals are not well defined, but roughly translated to achieving a particular ecological process (e.g., productivity, suite of processes, and/or desired community composition) (Lindenmayer et al. 2008, Ritz et al. 2009, Caporaso et al. 2010, German et al. 2011). The systemic and integrated impacts of urban expansion and ecological restoration highlight the need for research on the mechanisms of belowground processes in ecosystem functioning in managed urban areas for sustainable ecosystem management.

Decomposition

Decomposition is a vital ecological process whereby dead organic material is degraded into essential elements by a diverse array of soil fauna. Fungi and other soil organisms decompose dead plant material and therefore control a critical step in nutrient cycling. Previous studies have described how litter quality, soil fertility, disturbances, plant community composition, and climatic factors feed back to influence litter decomposition in natural areas or agricultural ecosystems but rarely are they considered together in space and time. In contrast, there are few comparable studies in urban or restored systems. Historic land use and current land management practices likely influence plant community composition and thus litter quality, microbial community composition and functioning, and soil factors, all of which feed back to influence litter decomposition and nutrient cycling. Restored systems provide the unique opportunity to simultaneously test these factors because of the inherent site disturbances and alterations in soil and plant communities that accompany restoration. Further, success or failure of restorations may be linked to successful restoration of ecological processes, such as decomposition and nutrient cycling.

While soil microbes (bacteria and fungi) are large drivers of decomposition and biodiversity, very few of these microscopic organisms are described in science (Wieder and Lang 1982, Tedersoo et al. 2014). Despite the importance of soil fungi in global nutrient cycles, little is known about the patterns of fungal community structure relative to native plant community or ecosystem structure and function, and even less is known of their corresponding feedbacks to ecosystem function within the context of restoration. Historical land use and current land management patterns likely influence the soil microbial community through direct and indirect actions of soil disturbance, chemical introduction, and plant species manipulation. Decomposition and soil biological diversity are recognized as important to ecological function and overall biological diversity, but the impacts of active land management on this process are understudied.

Soil bacteria and especially fungi are the largest drivers of decomposition owing to their capacity to degrade litter substrates by enzyme activity (McGuire et al. 2010). Several authors have suggested that variation among fungal species or physiological characteristics of fungal communities may be factors regulating their diversity in natural systems (Atkinson 1988, Atkinson 2001, Asbjornsen et al. 2005, Ashworth et al. 2006). Laboratory and greenhouse-based studies indicate that fungal taxa can differ in their response to use of C sources (Ferry 1968, Atkinson 1988, Durall 1994, Tibbett 1998, Gramss 1999) and ability to compete with other fungi (Baar 2000, Conway 2000), and thus fungal and plant community diversity would likely co-vary. However, most of these studies are conducted in controlled environments (McGuire and

Treseder 2010), so extrapolating the applicability of these traits to fungi in remnant or urban restored systems is problematic.

Recent studies indicate that the diversity and composition of fungal communities can be altered by nitrogen deposition, land use change, and disturbance, all factors that occur in urban restorations. Litter accumulation and altered soil nutrient availability can be significant drivers of plant species richness (Fang et al. 2012). Areas invaded by non-native invasive plants and those formerly used for agricultural production are associated with high soil fertility and altered soil faunal communities and decomposition rates. These effects can persist following invasive plant removal thereby hindering the successful restoration of native plant communities as well as ecosystem functions (Heneghan et al. 2009, Weidenhamer and Callaway 2010, Iannone III et al. 2012).

Soil biota modifications that are associated with altered plant communities and can have both short and long-term consequences for plant community composition. In many cases, changes to soil communities resulting from exotic species-dominated plant communities can alter ecosystem processes in ways that facilitate further invasive species' competitive advantage over natives, regardless of nutrient availability (Reinhart and Callaway 2004, 2006, Cui and He 2009).

Studies of decomposition in urban- rural gradients and in urban areas show that litter decomposition increases with increasing N deposition and that N mineralization (Liu et al. 2010) and decomposition is often higher in urban than rural systems (Steinberg et al. 1997, Pouyat and Carreiro 2003, Nikula et al. 2010), but not always (Pavao-Zuckerman and Coleman 2005). Decomposition rates also co-varied with the abiotic environment and litter quality (Pouyat and Carreiro 2003). However, there is less information on the mechanistic basis of leaf litter decomposition or links between decomposition and soil nutrient availability in urban systems (McDonnell et al. 1997). Given our limited understanding of decomposer community structure and function, but acknowledging their critical role in nutrient turnover, it is clear that understanding above- and belowground interactions are necessary in describing the ecosystem level impacts of plant invasion and restoration.

The C: N ratio of litter substrates strongly influences its decomposition rate (Swift et al. 1979). Plant community composition has the potential to influence decomposition because different plant life forms or species provide different quantities and qualities (C: N) of litter (Liao et al. 2008, Zhang et al. 2008). Shifts in fungal community composition have been noted in response to tree species (Trappe 1977, Smith and Read 1997, Massicotte 1999, Ferris et al. 2000), litter quality (Koide 1998, Nilsson 1999, Conn and Dighton 2000), the stage of litter decomposition (Mitchell and Millar 1978, Rack and Scheidemann 1987, Ponge 1991, Klironomos et al. 1992, Senthilkumar et al. 1993, Holmer and Stenlid 1996, Holmer et al. 1997, van Maanen and Gourbiere 1997, Frankland 1998, Pasqualetti et al. 1999), as well as succession following disturbance (Last et al. 1984, Termorshuizen 1991, Baar 1996), fire (Jonsson et al. 1999, Stendell et al. 1999, Claridge et al. 2000), land use change (Boerner et al. 1996), and forest openings (Kranabetter and Wylie 1998, Claridge et al. 2000). Most of these studies concluded that any changes in community composition could affect various aspects of nutrient cycling, such as primary productivity, plant nutrient status, and decomposition rates. While this information is valuable, these studies were undertaken in native systems or in controlled laboratory or greenhouse studies so that the ability to use this information in restored communities is limited.

Despite decades of research into both the basic ecological drivers of leaf litter decomposition and restoration and natural area management, our understanding of the impacts of restoration practices on belowground processes such as decomposition remains extraordinarily poor. Restoration experiments often focus on the impacts of specific restoration activities such as reducing exotic plant invasion and restoring native plant biodiversity, but rarely investigate the impacts of management activities on belowground processes that can structure the plant community. In this Chapter, I focus on the role of fungi in coupling above- and belowground processes, because fungi are major components of ecosystems and can be powerful drivers with both positive and negative effects on nutrient cycling, plant interactions, and diversity.

My research fills gaps in our understanding of the feedbacks generated by interactions between the fungal community, litter quality, and soil fertility on nutrient cycling and provides the first comprehensive analyses of the controls over decomposition in restored urban grasslands. These insights are critical to understanding the feedbacks created by belowground processes to changing environmental parameters (e.g., plant species composition, soil nutrient availability) in restoration processes but will also be broadly applicable to understanding the effects of plant species invasion, nitrogen deposition, and increasing anthropogenic disturbances on ecosystem function.

In this chapter, I examine the interconnected hypotheses that historic and current land management practices and differences in plant tissue chemistry influence decomposition and the function and community composition of decomposer fungi in remnant and restored urban grasslands. I ask the following questions: 1) Are there differences in decomposition rates among land use history, duration of land management, and leaf litter types? 2) Are there differences in fungal community functioning (enzyme activity) among land use history, duration of management and leaf litter types? 3) Are there differences in fungal community composition among management types?

To address these hypotheses, my study comprises species-, community- and ecosystem-level analyses in an urban context. Study sites include remnant and former row-crop agricultural fields that have been restored to tallgrass prairie across a restoration chronosequence within a 70-km radius of downtown Chicago. These sites are relatively constant in climate and management techniques but vary in plant community composition and management duration. I employ a field study of leaf litter decomposition using three litters of contrasting quality (grass, forb, and legume) in mesh bags. I link litter decay with litter chemistry, microbial function using enzyme assays, and fungal diversity using metagenomics. I also evaluate these results as they relate to land-use history and land management duration (Figure 1). This research explores potential interactions between grassland management and microbial diversity and functioning and will consider the implications for natural, restored, and increasingly urbanized ecosystems.

The Chicago metropolitan region is an ideal location to investigate how aboveground management practices influence plant community composition and belowground processes as it has a long history of ecological restoration and a general similarity in management techniques that are replicated across the region. This context allows for a replicated, landscape-scale, natural experiment capitalizing on the restoration history of natural areas across the region in a tradition that is well documented in ecological history.

Methods

Site Selection

This study occurred on 23 grassland sites that are a part of the Chicago Wilderness Land Management Research Program (Chapter 1, Figure 2) and utilizes a space-for-time experimental design based on sites identified by land managers as being representative of one of four management categories: 1) control, sites that are currently not managed and considered by land managers to be degraded and dominated by non-native species; 2) early restorations, sites that were restored within the last 10 years; 3) intermediate restorations, sites that have been under restoration for at least 10 years; and 4) references, sites that are identified by land managers and theoretical reference or target ecosystems. The grasslands include former row-crop agricultural prairie restorations and prairie remnants (Table 1). Sites were selected as having similar soil moisture, texture (silty clay or silty clay loam), and nutrient availability (Table 2, Table 3, Appendix C, Table 1).

Soil Analyses

Soil texture was determined using a 5% sodium metaphosphate dispersing solution and a hydrometer (Robertson et al. 1999). Gravimetric moisture content was measured by drying soils in an oven at 105^{o}C following standard soil methods (Robertson et al. 1999). Soil nutrient availability was determined using commercially available ion exchange membranes (Plant Root Simulator, hereafter, PRS^{TM} probes) (Johnson et al. 2007). Four of each cation and anion PRS^{TM} probes were buried at each study site for 28 days in the late summer of 2009 and 2010. PRS^{TM} probes were then analyzed for NH_4^+, NO_3^-, P, K, S, Mg, Fe, Al, Mn, Cu, Zn, B and Pb as µg/cm^2/28days (Appendix C, Table 1).

Vegetation

Functional vegetation by cover of native grasses, non-native grasses, native forbs, non-native forbs, sedges and rushes, woody stems, detritus, moss, and bare-ground were estimated using a modified Whittaker plot method and the Braun-Blanquet cover-class system as described in Chapter 1. Median cover class values were used for ordination figures and are summarized in Appendix C, Table 2.

Leaf Litter Decomposition

Dried leaf litter was collected from a remnant prairie within the study site region (but not included as a study site) in mid-November 2012, when most prairie vegetation was dead standing biomass. Fiberglass mesh litterbags, each measuring 17 x 17 cm were filled with 6 – 8 grams of one of the following litter types: *Andropogon gerardii* (C: N 101 ± 3), *Rudbeckia subtomentosa* (C: N 70 ± 3) or *Baptisia australis* (C: N 59 ± 1). These species represent commonly occurring species of graminoid, forb, and legume, respectively, in both native and restored sites. Eighteen bags of each species were secured to the soil surface, under any existing detritus and leaf litter, using stainless steel landscaping stables in March 2013, as soon as the soil surface was not frozen (Figure 3). Three bags of each species were removed in June, September, and November 2013 and mid-November, 2014. Two extra litterbags of each species were removed immediately to account for initial moisture content and potential mass loss in transport and installation. Sixty litterbags per site and 1,440 litterbags throughout the study were placed in the field for the 2-yr study period. Collected leaf litter was freeze-dried in glass vials at Northwestern University and weighed to determine total mass loss.

Characterization of microbial function

Enzyme assays produced by fungi and associated with the decomposition of simple C compounds (α-glucosidase, AP, β-glucosidase, BG), chitin (N-acetyl-β-glucosaminidase, NAG), and oxidative activity (phenol oxidase, POD) in litter was determined using fresh litter extraction methodology developed by (Carnovale 2013) modified from (Sinsabaugh et al. 1991, Allison 2005). Collected litter was processed for enzyme assay within 48 hours of collection. A subsample of 0.1 to 0.3 g of litter was suspended with 1.0 mL of 50 mM sodium acetate buffer solution and homogenized using a bead beater for one minute the day of and again the morning after collection, then diluted and suspended for 30s using a vortex to a total of 10 mL sodium acetate buffer. Triplicate 50 µL of homogenate was combined with 150 µL of substrate and incubated at 30˚C for 1 (AP, BG, POD), 2 (NAG) or 4 (CBG) hours in 96 well plates. Absorbance of plates was then read in an Epoch well plate reader at 405 nm (450 nm for POD) and activity is expresses in µmol of substrate hydrolyzed per hour per gram of dry litter, averaged by sample, and then by litter type for each site and collection.

Amplicon library preparation

A subsample of litter was frozen the day of collection for subsequent DNA extraction, amplicon library preparation, and high-throughput sequencing to profile the microbial communities associated with each litter type during the temporal sequence of decomposition. At least one of each litter type was collected from four sites representing the treatment extremes - unmanaged restorations (old-fields) and prairie remnants and reference restorations and remnants for a total of 16 samples was used for fungal community analysis. Total DNA was extracted from each sample using Mo Bio PowerSoil kits (Mo Bio, Carlsbad, CA, USA) following manufacturer protocols. Fungal-specific primers BITS/ITS2_Kyo1 (Bokulich and Mills 2013), modified to include Miseq-compatible adapter sequences and unique 12 base Golay error-correcting barcode sequences, were used to amplify the ITS1 region of fungal rDNA. Libraries were produced with a single step PCR reaction using MyTaq HS Mix hot start taq polymerase mastermix (Bioline, London, U.K.). Triplicate amplicon libraries for each sample were produced, pooled, and taken to Argonne National Laboratory for quantitation by picogreen assay and fluorimetry, combination into an equimolar sequencing library, cleaning with a Mo Bio PowerClean kit following manufacturer's protocols, and analysis on an Illumina Miseq using the version 2, 2x250bp paired end chemistry.

Bioinformatics and sequence analyses

The resulting sequencing reads in fastq format were processed, quality filtered, and analyzed using the QIIME pipeline (version 1.8; Caporaso et al. 2010). Only 16% of paired forward and reverse reads were successfully assembled, so further sequence read processing and community analyses were done using only the forward reads. Sequence reads were demultiplexed and quality filtered using default parameters except that a phred score of 20 was used as the minimum acceptable threshold, and up to two errors in the barcode sequence were allowed for reads to be retained. Reads were clustered into operational taxonomic units (OTUs) at the ≥97%sequence similarity level using an open-reference OTU picking strategy with the UNITE 97% species hypothesis database release for QIIME version 6 (Koljalg et al. 2013) used as the reference database. Sequences of probable non-target taxa and artifacts were excluded by blasting OTU representative sequences against the UNITE database with a minimum acceptable e-value of 10^{-50} and 97% query coverage. Taxonomy was assigned to OTUs using the QIIME implementation of RDP Classifier (Wang et al. 2007) retrained using the UNITE database. Summary plots of read abundance by assigned taxa, alpha rarefaction curves, and Bray-Curtis and Jaccard's community distance metrics were produced in QIIME. Subsequent statistical analyses of community relatedness were performed in the R studio (2015) with the *vegan* package (Oksanen et al. 2015).

Statistical Analysis

All data analysis was conducted using R statistical environment (R Core Team 2013). Differences in soil characteristics were determined using ANOVA with management category or land-use history as explanatory variables. Median vegetation cover classes as well as enzyme activity were analyzed using NMDS and differences in plant community assemblage and enzyme activity with land management category and leaf litter type as explanatory variables was determined using Adonis with 10,000 permutations.

Results

Soil characteristics and plant communities

Soil moisture, inorganic nitrogen (NO_3^- and NH_4^+), ammonium (NO_3^-), nitrate ($NH4^+$), and potassium (K) availability was similar across all sampled sites (Table 2, Table 3, Appendix C Figure 1). Phosphorus availability was similar across all management categories (Table 2) but more than four times greater in restorations than remnants (Table 3, Figure 5).

Plant communities differed by land-use history ($p = 0.003$, $R^2 = 0.06$, Figure 6a.) and management duration ($p < 0.001$, $R^2 = 0.19$, Figure 6b.) and there were interactions between the two ($p = 0.004$, $R^2 = 0.05$).

Decomposition

After 20 months, mass loss differed by litter type ($p < 0.001$, $F = 9.6$) but not by land-use history ($p = 0.20$, $F = 1.7$) or management duration ($p = 0.41$, $F = 0.70$) and this trend was similar for all collection dates (ex. Appendix C, Figure X). Throughout the 4 collections, the *R. subtomemtosa* mass loss remained the greatest, but these differences were only significant at the final collection at 20 months ($p < 0.05$, Figure 7, Figure 8). *A. gerardii* mass loss was significantly lower than the other two litter types at the first collection but by the final collection, was indistinguishable from the legume, *B. angustifolia* (Figure 9).

Microbial diversity

Enzyme activities were not significantly different by litter type (Figure 10), land-use history (Figure 11), nor management category (Figure 12). Fungal community composition differed by management type ($p = 0.012$, $R^2 = 0.084$, Figure 13) as well as by leaf litter type ($p = 0.029$, $R^2 = 0.15$, Figure 14).

Discussion

Land-use history and management duration influence plant community and fungal composition, but not decomposition rates, microbial enzyme activity, nor soil nutrient availability, with the striking exception of soil phosphorus. The similarity in decomposition rate and enzyme activity but differences in fungal decomposer community composition suggests that there is functional redundancy in the decomposing communities. While several different species and combinations of species are responsible for the breakdown of different types of leaf tissue, they use the same or similar enzymes to achieve this process of tissue decay. Ultimately, the rates of leaf litter mass loss, regardless of fungal community composition are indistinguishable. The functional redundancy concept in ecology helps explain potential buffering effects of ecosystem function typically associated with species loss because multiple species may have overlapping niches in a given ecosystem. While generally well documented in the literature (Yin et al. 2000, Rosenfeld 2002, Allison and Martiny 2008, McGuire et al. 2010, McGuire and Treseder 2010), there is debate about how important the role of functional redundancy is in determining species diversity and ecosystem function (Loreau 2004), as well as whether this redundancy can serve as a buffer for species loss (Fonseca and Ganade 2001).

There is a need for further research linking species identity to ecological function in order to understand the potential impacts of species loss and prioritize management focused on maintaining ecosystem function (Rosenfeld 2002). Similarly, other studies have found that changes in enzyme activity either were not or were very weakly correlated with genetic structure of soil bacteria in managed grasslands (Patra et al. 2006) and that soil decomposing organisms are largely generalists with high degrees of functional redundancy (White et al. 2004). However, this finding is in constrast to studies that found differences in function, but not taxonomy in soil organisms (Pavao-Zuckerman and Coleman 2007), and where greater species microbial diversity resulted in increased cellulose decomposition (Wohl et al. 2004).

Drivers of Decomposition

Leaf litter decomposition was driven by litter type but not land-use history or management duration. The chemical components of leaf tissue vary by plant species as well as local site conditions. These differences can work independently or combine to influence decomposition rates and microbial communities (Aerts and de Caluwe 1997, Sariyildiz and Anderson 2003, Meier and Bowman 2008). Decomposition rates are driven by leaf litter chemistry more than plant species diversity when both are considered (White et al. 2004, Meier and Bowman 2008). However, functional diversity, rather than species richness of plant communities may also have an impact on decomposition rates (Scherer-Lorenzen 2008) by changing the quality of substrate availability (Spehn et al. 2000). In my study, differences in decomposition were not clearly related to basic definitions of litter quality, as hypothesized. My results suggest that defining litter quality by C: N is too simplistic to accurately predict decomposition. More robust analysis of the chemical components of leaf tissue such as crude protein, dry matter digestibility, neutral detergent fiber, magnesium, phosphorus, cellulose, phenolics, lignin, hexose, and hemicelluloses may be needed to better determine which component or combination of components of leaf litter are primary drivers decomposition and soil microbial function (Aerts and de Caluwe 1997, Preston et al. 2000, Sariyildiz and Anderson 2003, White et al. 2004). Further, a more detailed understanding of the chemistry of leaf tissue would more directly link chemical components of leaf tissue to microbial enzyme activity (Allison and Vitousek 2004) and advance our understanding of relationships between aboveground plant community composition and the function and diversity of decomposing organisms.

The legume, *B. angustofolia* had the highest litter quality (lowest C: N) and was expected to decompose more rapidly than the other two litters (Taylor et al. 1989, Spehn et al. 2000, Milcu et al. 2008, Scherer-Lorenzen 2008), but remained intermediate to the grass and forb throughout the 20-month study. Mass loss of the forb, *R. subtomentosa* remained the greatest throughout the experiment, though those differences weren't significant until the conclusion of the experiment. As hypothesized, *A. gerardii*, which had the lowest leaf litter quality, was the slowest to decompose during the first season. However, this difference was only significantly different for the first collection, suggesting that for the other leaf litter types, initial mass loss is driven by the breakdown of simple compounds. By the end of the experiment, the mass loss of the low-quality grass was equivalent to that of the high-quality legume. This similarity after two complete growing seasons in the field suggests that the majority of the simple components of the leaf tissue had decayed, leaving more complex, difficult to breakdown compounds that are common in most herbaceous plants (Moorhead and Sinsabaugh 2006).

Differences in fungal community composition extracted from leaf litter differ by management duration and litter type. Control sites that were unmanaged, regardless of land-use history, had similar communities to each other, but differed from all managed sites. The fungal communities of all managed sites, regardless of management duration were more similar to each other than they were to the control sites. Similar studies have come to complimentary conclusions, where soil bacteria community composition is driven more by plant species or habitat type than management activities (Nacke et al. 2011). Other studies have found that there are important differences in microbial activity in response to short-term grassland management changes (Lovell et al. 1995), but my results indicate that more significant differences in microbial communities are driven by initial restoration activities rather than ongoing management activities. The relatively few replicates used for community analysis limits the strength of the conclusions drawn from these results, but this finding is in line with other studies that demonstrate that plant invasion influences microbial community composition in grasslands

(Jordan et al. 2008) and that these invasive species dominated soil communities are distinct from managed and reference sites (Clegg et al. 2003).

Management Influences Plant Communities

Differences in plant communities were more notable between land-use histories, where the confidence intervals did not overlap. Remnant sites were distinguished from restorations primarily by a greater coverage of sedges and rushes, while restorations were dominated by non-native grasses and forbs. Community composition of restorations were also more variable as visualized by a wide spread of sites in the ordination figure, while remnants are more tightly clustered, thereby having more similar plant community composition across all sites.

While statistically significant, vegetation differences by management duration were less distinct, with considerably more overlap in functional plant group cover. Management activities appear to shift the plant community from one that is dominated by non-native grasses, non-native forbs, and woody species to one that is dominated by native grasses, native forbs, sedges and rushes, and accumulated detritus. Duration of management activities appear to place plant communities on a trajectory towards the higher quality reference restorations, but these former agriculture sites remain distinct from remnant prairies regardless of time under management. Aboveground focused restoration efforts thus appear to achieve the primary goal of restoring native plant community structure toward a more native-dominated community, even if the community composition differs from remnant sites.

Further exploration of the drivers of leaf litter decomposition in managed urban grasslands over time could be achieved by using additional next-generation DNA sequencing with each litter collection and by a more in-depth analysis of the chemical composition of the leaf litter types. Moorhead and Sinsabaugh (2006) generated a model that demonstrates the functional and broadly taxonomic successional shifts of decomposer communities as easily degradable compounds diminish and more complex components of leaf tissue remain, but little work has focused on describing the species identities of these functional groups. With the emergence and increasing cost-effectiveness of next-generation DNA sequencing, future research that identifies the fungal communities that colonize decomposing tissues over time, as well as more detailed leaf tissue analysis can provide critical information linking fungal identity to ecological function (Schneider et al. 2012).

Agricultural Legacy

The long-term impacts of row-crop agriculture persists well after farming ceases, as evidenced by the dramatically elevated phosphorus levels in restoration sites compared to remnants. This difference is particularly concerning for conservation practitioners considering that some of the sites included in this study have been seeded with prairie species and out of agricultural production for several years. This dramatic difference of soil nutrient availability explain the significant differences in plant communities between the two prairie types and will likely continue to influence plant community assemblages, belowground activity, and above-belowground relationships.

In Chapter 2, I also observed that soil phosphorus availability was the only soil variable that significantly differed by land-use history and management duration. Considering all 60 grassland sites, phosphorus was nearly triple in former agricultural soils compared to remnants. In the subset of 19 grasslands chosen for this experiment, differences in soil available phosphorus was even more pronounced, as it was greater than four-times that of remnants. Plant communities in both the larger dataset as well as the subset used in this study differed both by land-use history and management duration, but the differences between remnants and restorations were more pronounced in this study. The lack of differences in all other measured soil properties between site treatments suggests that the legacy impacts of agricultural soil-fertility management practices result in pronounced differences in phosphorus, and that this soil characteristic can have substantial implications on restoration outcomes both above- and belowground.

The long-term legacy effects of row-crop agriculture, as evidenced by striking levels of phosphorus availability in the soil, is likely to have significant impacts on above- and belowground biodiversity, community composition, and their interactions. Previous studies demonstrate that N availability in former agricultural areas impacts aboveground productivity and diversity, and soil biodiversity, (Walker et al. 2004, Baer et al. 2005) and that high soil phosphorus levels are negatively correlated to plant and mycorrhizal abundance and diversity (Janssens et al. 1998, Alguacil et al. 2010, Ceulemans et al. 2014). Less is known about the implications of soil phosphorus availability on fungal abundance, diversity, function, and subsequent interactions with plant communities and prairie management strategies (Fierer et al. 2013).

This study fills gaps in our understanding of the impacts of row-crop agricultural, prairie restoration, and ecosystem management on plant communities, soil nutrient availability, decomposition, decomposing microbial communities, and their relationships. It also provides the first comprehensive analyses of these relationships in restored urban grasslands. The combination of field-ecology techniques combined with the use of next-generation DNA sequencing allows for significant insights into the identity of the fungal community driving decomposition in grasslands. This application is relatively new, but extremely promising in describing belowground biodiversity in prairies that could be used to improve restoration (Fierer et al. 2013). The genetic component of this study also allows for a taxonomic template of the direct and indirect responses of fungi to plant and soil controls as well as restoration practices.

In Chapter 1, I established a landscape scale framework to address above- and belowground impacts of restoration and land management in the region. In Chapter 2, I examined these questions on a broad scale, investigating differences and relationships between plant communities and soil properties. In Chapter 3, I focused on the relationships between shrub invasion and N availability in woodlands in a spatial context to guide future restoration activities that were invaded but had belowground characteristics that might facilitate or at least not hinder restoration success. In Chapter 5, I explored methods to reduce nitrogen availability following invasive shrub removal. In this chapter, I focused on a decomposition, a critical ecological process that very directly links above- and belowground communities in prairies. I have observed that in urban grasslands, nitrogen does not appear to be a strong ecological driver of above- and belowground community composition. However, the legacy impact of farming practices dramatically influenced phosphorus availability, the direct implications of which remain unclear. Similar to methods employed in Chapter 5, future studies that explore methods to reduce phosphorus availability in soils may provide insight into these relationships and how land managers may best employ novel soil management strategies in the early stages of prairie restoration. Restoration of soils and soil processes in prairie restorations may be essential to native plant species establishment, increased biological diversity, and long-term ecosystem resilience.

Chapter 5

The impacts of soil carbon addition on soil nutrient dynamics and European buckthorn (*Rhamnus cathartica)* re-invasion and growth

Abstract

European buckthorn *(Rhamnus cathartica)* invades woodlands and forests in the Northeast and upper Midwest of the United States. Once established, this large shrub often forms dense thickets and significantly diminishes native plant species diversity. Ecosystems inundated with buckthorn are associated with elevated soil N, altered ecosystem processes (accelerated decomposition and nutrient cycling), and greatly modified soil foodwebs that persist following buckthorn removal. I hypothesize that successful prevention of buckthorn re-invasion and the restoration of native plant communities will be promoted by reducing buckthorn's legacy effect of elevated soil N by employing management techniques that reduce soil N concentrations after buckthorn removal. I report results from a field–scale experiment conducted in a heavily invaded old-field site in Mettawa, IL. I examined the impacts of several established and novel buckthorn management strategies on ecosystem processes and vegetation outcomes. Results indicate that reinvasion by *R. cathartica* was significantly reduced when woody mulch (using mulch composed of *R. cathartica* wood, or a commercially available mulch) was incorporated into the soil. Bioavailable plant nutrient supply rates, measured using PRS™ probes were altered in all treatments. In the greenhouse, buckthorn germination, seedling growth, and transplanted sapling growth was significantly reduced in soils amended with either type of mulch.

Introduction

Invasive species are associated with modified ecosystem properties compared to ecosystems where native vegetation is dominant (Corbin et al. 2004, Hawkes et al, 2005). Areas invaded by non-native plants often exhibit elevated soil nutrient levels, altered soil faunal communities, and elevated decomposition rates, the effects of which are thought to persist following invasive plant removal, thereby hindering the successful restoration of native plant communities.

Areas invaded by non-native invasive plants can be associated with high soil nutrient levels, altered soil faunal communities, and elevated decomposition rates. These effects are thought to persist following invasive plant removal thereby hindering the successful restoration of native plant communities (Wilson and Gerry 1995, Suding et al. 2004, Yelenik et al. 2004, Heneghan et al. 2006, Rodgers et al. 2008, Weidenhamer and Callaway 2010). Elevated soil nutrients can contribute to an area's susceptibility to plant invasion and/or domination by rapidly growing, weedy species at the expense of more conservative species and this condition can persist following restoration (Davis et al. 2000, Heneghan et al. 2006, Dassonville et al. 2008, Iannone III and Galatowitsch 2008, Cherwin et al. 2009). Exotic species dominance can also alter soil microbial structure and function (Kourtev et al 2002). Modified belowground communities and nutrient cycling may have significant consequences for restoring a previously invaded ecosystem to a diverse native plant community. A literature review showed that most invasive plants only outcompete natives when resources are elevated or disturbance regimes are altered from their historical frequency (Daehler 2003).

European buckthorn (*Rhamnus cathartica,* L.) (hereafter buckthorn) is a non-native shrub that invades woodlands and forests in the Northeast and upper Midwest of the United States.

Ecosystems inundated with buckthorn are associated with elevated soil nitrogen (N), moisture, and pH, as well as modified soil faunal communities compared to non-invaded sites (Heneghan et al. 2007b). Restoration of buckthorn invaded areas is met with mixed results. Aboveground removal of the invasive shrub is occasionally followed by the establishment of a native plant community, but reinvasion is common. Studies suggest that these modified properties persist following removal of the invasive plant resulting in a "legacy effect." This legacy effect might facilitate reinvasion by the same or other non-native species, delaying the success of restoration actions where the goal is to increase native plant biodiversity. The barrier to consistent success in restoration of temperate woodlands and prairies invaded by buckthorn may lie in belowground modifications that sustain plant communities (Heneghan et al. 2008). These ecological processes often subtend the assemblage of aboveground and belowground ecological communities and contribute to the long-term sustainability of the ecosystem. The ultimate success of meeting many restoration goals may be hindered by neglecting these belowground processes.

Reinvasion following aboveground restoration techniques by buckthorn or other invasive woody and herbaceous species is likely due to modified ecosystem properties that persist following buckthorn removal, but this hypothesis has not been thoroughly tested in the field. For this reason, carbon (C) addition has been proposed as a method for immobilizing plant available N in order to increase the potential success of native species relative to non-native invasive species (Averett et al. 2004, Kettenring and Adams 2011)

Soil carbon addition has been proposed as a viable restoration method for immobilizing plant available N in order to increase the potential success of native species relative to non-native invasive species (Blumenthal et al. 2003a, Averett et al. 2004, Corbin and D'Antonio 2004, Kulmatiski and Beard 2006, Cherwin et al. 2009). These experiments have varied methods, have been limited to small study plots, short lived herbaceous species, and the effects on soil nutrient availability are not consistent. While the methods and results vary, the general success of C addition experiments in managing woody invaders yield some promising initial results.

The addition of C to soils is expected to result in a reduction of available N through microbial immobilization, resulting in reduced establishment and growth of non-native species in tallgrass prairies (Blumenthal et al. 2003b, Perry et al. 2010). Comparable results were demonstrated in Minnesota when sawdust addition was used in conjunction with seeding, resulting in reduced establishment and subsequent growth of *Phalaris arundinacea* with no negative effect on the target community (Iannone et al. 2008). A similar study on former agricultural land showed that sawdust addition resulted in a reduction in N mineralization and significantly reduced exotic but not native plant biomass by the second growing season (Averett et al. 2004). Soil amendments that reduce nutrient availability can also have positive effects on the relative success of seeded natives to weedy non-natives compared to restorations where no amendments were employed (Cherwin et al. 2009).

Generally, soil carbon studies have resulted in decreased establishment, cover, growth, or biomass of exotic plants (Morghan and Seastedt 1999, Blumenthal et al. 2003b, Averett et al. 2004, Perry et al. 2004, Prober et al. 2005, Bleier and Jackson 2007, Iannone III and Galatowitsch 2008, Iannone III et al. 2008, Cherwin et al. 2009, Iannone III et al. 2009). Other studies have explored the use of harvesting rapid growing annual grasses as cover crops to reduce soil nutrient availability with mixed results. As such, this technique is not recommended as a reliable restoration tool (Iannone et al. 2008).

While these results are promising, they often occur in small, experimental test plots. Thus, their large-scale impacts on plant communities and the feasibility of implementation by land managers has not been fully studied. Further, the use of soil amendments in restoration has not yet occurred in urbanized areas where soil disturbance, frequency of non-native plant introduction, and nutrient availability are often greater. While land managers of the region acknowledge that restoration efforts are often hindered by complex, belowground components, there currently exists little to no information no how to effectively implement management strategies that address these larger issues. The lack of scalable and practical research is why many are hesitant to experiment with novel approaches fearing that they won't work or might be more harmful than standard management approaches with more predictable outcomes. This uncertainty is precisely why this study is essential to elevate the practice of ecological restoration from exclusively aboveground methods that require regular and often intensive follow-up to a more holistic approach that accounts for the ecosystem processes. The use of soil amendments in restoration has not yet occurred in urbanized areas, where soil disturbance, frequency of non-native plant introduction, and nutrient availability are greater

In this chapter, I explore the larger-scale impacts of restoration efforts that directly manipulate soil through C addition in conjunction with the varied seed mixes compared to regionally established best management practices in a field study in the suburbs of Chicago, IL. I hypothesize that successful restoration will be promoted by employing management techniques that reduce soil nitrogen concentrations after buckthorn removal.

Methods

Experimental Site

The experiment was conducted on a 2.8-ha site in Mettawa, IL, approximately 30 miles northwest of downtown Chicago, IL. The site was used as a horse pasture until 1990, when which time it was abandoned and became a monoculture of buckthorn. Approximately 2500m^2 of the site is allocated to this experiment (Fig. 1). The Village of Mettawa contracted with two commercial restoration companies to manage the remainder of site.

Experimental Design

Each experimental unit was a 52-m2 hexagonal plot (Fig. 1). Treatments were arranged as a randomized block design of 5 blocks (arranged along a suspected hydrological gradient) and 8 treatments (Table 1).

Removal, soil manipulation and seed treatments

Treatment 1: Control (C). No treatment was applied. These plots of standing buckthorn serve as a control for other all other buckthorn removal and soil manipulation treatments.

Treatments 2-8: Buckthorn removal. All soil and seed treatment plots received the same buckthorn removal treatment that follows the best management practices of the region. Buckthorn stems were cut by hand using loppers and bow saws. Cut stumps were then treated with Garlon 4 (Triclopyr: 3,5,6-trichloro-2-pyridinyloxyacetic acid, butoxyethyl ester) with a red or blue dye and kerosene carrier.

Treatment 2: No mulch, native seeds (NS). This treatment best replicates standard post-buckthorn removal practices in the region. In the late fall following buckthorn removal, a native species seed mixture of 3 species of grasses at a rate of 1.07 g/m^2 and 33 species of forbs at a rate of 0.39 g/m^2 (Appendix C, Figure 1) was hand-broadcast seeded across the plots.

Treatment 3: No mulch, cover crop (ILM). This treatment uses a spring cover crop of pasture grasses *Phleum pretense, Dactylis glomerata*, *Bromus inermis* and *Avena sativa* at a rate of 16.8g/m^2. Cover crops should retard the growth of less desirable weeds (Ilnicki and Enache 1992, Shebitz and Kimmerer 2005), and harvesting cover crops will reduce soil N.

Treatment 4: No mulch, commercial corn seeds (Zm). Cultivation of corn depletes soil N (e.g. Evanylo and Alley, 1998). Commercially available corn seeds were pre-treated with fungicide and planted every 0.2m, in rows spaced 0.61 m apart by hand. No water or fertilizer was used following planting. All aboveground biomass was harvested in the fall for two consecutive years.

Treatment 5: Commercial mulch, native seeds (M). The use of mulch and other low-quality (high C:N) substrates as a soil amendment in restoration has become prevalent (Bear et al 2006). Cellulose is a recalcitrant substrate and nitrogen is immobilized by the microbial community as it decomposes, reducing the availability of limiting nutrients for plant growth. This management technique can reduce colonization by non-native species in prairie restorations (Baer et al. 2003). Commercially available mulch (C: N = 106) was rototilled into the soil at a rate of 2.6 kg dry mulch/m^2, followed by hand-broadcast of the same seed mixture and rate as applied in Treatment 2. This treatment serves as a comparison of the buckthorn mulch treatments (6 and 7), since mulching buckthorn onsite is not feasible or permitted in all natural areas and thus an alternative source of mulch might need to be imported as a substitute.

Treatment 6: Buckthorn mulch, native seeds (Tg1). The most readily available source of cellulose in restoration plots is mulch prepared from the cut buckthorn (C:N = 71), I chipped all buckthorn onsite and used a rototiller to incorporate it into the soil at 210-220 kg per plot (average of 3.5 kg dry mulch/m2), a rate similar to those effective elsewhere (Averett et al. 2004). Plots were then planted with native seed.

Treatment 7: Buckthorn mulch, cover crop (Tg2). Buckthorn mulch was incorporated into the soil as described for Treatment 6, but seeded with the species and rate as described in Treatment 3.

Treatment 8: Leaf Removal (LW). Removing buckthorn leaves is hypothesized to reduce densities of earthworms, whose ecosystem effects are postulated to foster buckthorn germination and growth and may be an important source of N in upper soil horizons (Heneghan et al. 2002, 2006b, Frelich et al. 2006). This treatment does not test a management practice, but rather addresses the more basic question how buckthorn leaf litter influences soil N, earthworm populations and buckthorn growth. This treatment was never fully implemented as the leaves were remained on trees well after most natives had senesced, almost immediately covered by snow or frost, and then decomposed during any thaw events through winter.

Soil analyses

Soil moisture, pH, total C and N were measured using Standard Soil Methods for Long-Term Ecological Research (Robertson et al. 1999). Labile soil nutrients were determined by placing two paired subsamples of commercially available Plant Root Simulator™ probes (Western Ag Innovations, hereafter, PRS™ probes) in each plot. The probes were analyzed for nitrate-N, ammonium-N, P, Ca, K, S, Mg, Fe, Al, Mn, Cu, Zn, B, and Pb. Probes were installed in the fall of 2008, spring 2009, and fall 2009.

Reinvasion

Buckthorn reinvasion, which included total number of seedlings, saplings, and resprouts was counted in each plot using three randomly distributed 0.25 m^2 quadrats per plot in the last week of July or first week of August each year from 2008 to 2012. No distinction was made between seedlings and saplings in 2008 as all individuals were under five cm in height and were assumed to be new seedlings. In the subsequent years, seedlings were identified as individuals with cotyledons still present. All other free-standing individuals were counted as saplings, regardless of height. Resprouts were counted using the number of new stems emerging from one cut stump in all years. These same measurements occurred in control plots, where notes of densities of adult trees were also taken.

Greenhouse Study

Buckthorn saplings were collected from Mary Mix McDonald Woods at the Chicago Botanic Garden (CBG) in Glencoe, IL in late June 2009. Sapling roots were rinsed, gently towel dried, weighed, and planted into randomly assigned soil treatments. Soil treatments include field collected soil with no mulch, buckthorn mulch, and commercially available mulch to best replicate field conditions in a controlled environment (Table 2). Once planted, each sapling was placed randomly in trays in the greenhouse at CBG and watered twice daily for 10 weeks (Figure 4). Stem height and leaf number were measured periodically for 7 months. In January 2010, 64 randomly selected saplings were harvested, rinsed, and dried to determine total dry biomass. Replicate samples of each soil type was tested for gravimetric water content, and NO_3^- and NH_4^+ using 2M KCl extractions and colorimetric analysis with a HACH DR 5000 Spectrophotometer and reagents (Robertson et al 1999) in at planting and harvesting.

Seeds from buckthorn were collected from natural area edges in Lake County, IL and planted into the same soil mixtures as the field-collected saplings (Table 2) and left to germinate in seedling flats in the greenhouse at CBG. Seedling emergence was observed and counted every three days. All seedlings with at least two true leaves (120 total) were transferred to larger pots in the same soil mix as before and moved to the greenhouses at DePaul University in October, 2009. Height and leaf number were measured at the time of transfer and every three weeks thereafter. Dry biomass was determined at the end of the experiment in January 2010.

Statistical Analysis

Differences in soil nutrient availability among treatments was determined using Analysis of Variance and treatment as factors. When differences were significant, pairwise comparisons were made using post-hoc Tukey’s honestly significant difference (HSD) to determine difference between treatments. Analysis was conducted using SAS 9.1.3 (SAS, 2011)

Reinvasion difference was determined using a repeated measures mixed effects model with plot nested within block and soil manipulation, seed type, and year as explanatory variables. *A priori* contrasts were used to compare difference in reinvasion between soil amended and non-amended plots and between mulch types. Analyses were conducted using R Studio (2015).

Results

Reinvasion

Buckthorn seedling and sapling density was significantly higher in control plots, where adult buckthorn trees were not removed, compared to all treatments plots ($F = 26.23$, $p < 0.0001$). Control plots, were excluded from further reinvasion analyses. Total buckthorn reinvasion from 2008 to 2012 was significantly impacted by mulch ($F = 7.49$, $p = 0.004$) and year ($F = 5.99$, $p = 0.0002$) but seed mix was not significant ($F = 0.27$, $p = 0.79$). *A priori* contrasts comparing all mulch treatments with all non-mulch treatments were significant ($p = 0.0016$) but there was no significant difference in reinvasion between the commercial and buckthorn mulch ($p = 0.42$, Figure 5).

Soil nutrient availability

One year after the installation of the treatments, there was significantly lower Calcium (Ca) availability in the control plots that in the no mulch/native, buckthorn mulch/covercrop, commercial mulch/native, and no mulch/corn treatments ($F = 3.25$, d.f. 6 $p < 0.02$). Although buckthorn mulch/native and no mulch/covercrop did not differ significantly from the control. There was a significant difference in Ca availability ($F = 3.76$, $p < 0.02$) across the assumed moisture gradient. Differences in Ca availability between plots planted with corn and the control plots were also detected in fall of year two ($F = 2.56$, d.f. 7, $p < 0.5$). When all mulched plots were considered together, they had significantly greater Ca availability than all other treatments ($F = 9.89$, d.f. 1, $p = 0.01$), though there were no differences detected between the commercial and the buckthorn mulch.

One year following the start of the experiment, Zinc (Zn) was elevated in all treatments compared to the control plots ($F = 4.9$, d.f. 6 $p < 0.01$). When all mulched treatments were considered together Zn availability was greater than in all treatments ($F = 5.89$, $p < 0.5$) and those differences were even greater in plots with buckthorn mulch ($F = 22.41$, d.f. 1, $p < 0.001$). After two years, treatment differences remained significant ($F = 5.97$, d.f. 7, $p < 0.001$), and mulch plots differed from the control plots ($F = 16.92$, d.f. 1, $p < 0.001$).

Phosphorus (P) availability was elevated in buckthorn mulch plots compared with a all others ($F = 5.15$, d.f. 6, $p = 0.01$) in the first year and these differences between treatments in P availability persisted into the spring and fall of the second year ($F = 6.86$, d.f. 7 $p < 0.001$, Figure 6). All mulched plots differed significantly from the control plots ($F = 21.60$ d.f. 1, $p < 0.001$). There was no difference between buckthorn and commercial mulch plots.

There were no differences between the treatments in total inorganic nitrogen (NH_4^+ and NO_3^-) availability for in the first or second growing seasons (Figure 7).

After two years, all treatments had elevated sulfur (S) availability compared with control plots ($F = 16.46$, d.f. 7, $p < 0.0001$). All mulched treatments considered together differ from the control plots, though there was no difference between the buckthorn mulch and commercial mulch treatments.

After two years, soil available lead (Pb) was significantly lower in control plots compared all treatments ($F = 6.57$ d.f. 7 $p < 0.001$). The pattern for aluminum (Al) availability after two years was the opposite, with significantly more Al available in control plots than the treatments ($F = 17.19$ d.f. $p < 0.001$). Cadmium (Cd) availability was also higher in control plots compared to in treatment plots ($F = 2.65$, df 11, $p < 0.05$).

Greenhouse Study

Saplings in mulch-free soil gained an average of 5.68 leaves from June to October, while saplings in mulch amended soils either maintained the same leaf number or lost leaves (Figure 8). Non-mulched saplings also grew taller than saplings grown in mulch, but heights were similar regardless of mulch type (Figure 9). Biomass change in saplings without mulch was nearly 23 times those grown in both commercial and buckthorn mulch soils, with no difference between the two mulch types (Figure 10).

More seeds germinated in non-amended soils than in mulched soils, and germination was lowerd buckthorn mulch soils with a similar pattern for biomass gain during the seven month growing period (Figure 11). Seedlings also gained significantly, on average more than twice as many, leaves when germinated and grown in un-mulched soils while those in mulch-amended soils lost an average of one leaf per seedling (Figure 12). The gravimetric water content was highest in the buckthorn mulch and lowest in the no mulch and commercial mulch mixtures before planting. After planting, the water content continued to be lower in the no mulch but higher in both mulch pots.

Discussion

Both field and greenhouse experiments indicate that the addition of mulch to soils following aboveground invasive shrub removal may lead to a reduction of reinvasion by new seedlings as well as reduced growth of saplings that may have been missed during the initial adult tree removal. The lack of differences between buckthorn and commercially available mulch, in both buckthorn reinvasion well as for most soil nutrient availability also suggests that woody material generated on-site or brought in material from nearby tree removal projects, commercial sources, or potentially any economically feasible source of low C: N material would achieve goals of reducing woody shrub reinvasion following aboveground removal. The results of this study suggest that the addition of mulch can enhance the restoration process by delaying, but not inhibiting, buckthorn germination and subsequent growth, though the mechanisms and soil nutrient availability changes were not as expected from previous carbon amendment studies.

Soil Nutrient Dynamics

The analysis of soil nitrogen availability is a focus of many studies examining the efficacy of incorporating material of low carbon quality (e.g., wood mulch) into soils as a potential restoration tool. This is because these treatments are hypothesized to reduce nitrogen, elevated in soil as a consequence of anthropogenic atmospheric input or as a legacy of fertilizer use in agricultural land. Nitrogen elevation is known to be a factor in some invasions and in a concomitant loss of native species. Defertilization (N reduction) in circumstances where land is managed for the protection of biodiversity may lead to a reduction in invasion and an increased prevalence of species of conservation significance. These treatments were designed to reduce the availability of soil nutrients, especially nitrogen, and thereby modify the structure of the plant community in revegetating plots in this manipulative field experiment.

Soil C amendments did not significantly reduce available N as expected, but plant nutrient supply rates were altered. Previous studies demonstrate reduction of available N following the addition of low C: N material to the soil, but our results are not consistent with these findings. Use of C addition to reduce soil nutrient availability associated with an invaded natural areas is becoming common in practice, but uncertainty still remains regarding the relationship between plant invasion and elevated soil nutrient levels. Studies demonstrating the utility of C addition in restoration often neglect to investigate the impacts of this soil manipulation on other important soil components, which, as we demonstrate, can be quite significant and may influence biogeochemical cycling.

For some of the nutrients measured in this study, availability was indeed reduced with C addition. However, these effects were not consistent over the two years, with the exception of phosphorus availability, which increased in plots that had received C addition. In this study, I included the analysis of the availability of several nutrients other than nitrogen. These included a range of ecologically significant anions and cations as well as trace and heavy metals including aluminum, cadmium, lead, and zinc.

The elevated phosphorus in mulched plots by the end of the second year is especially remarkable, as the role of buckthorn presence or removal in the phosphorus cycle has not, to date, received significant attention before. Similarly, the observation that trace metals were elevated in treated plots is seemingly a novel observation. Buckthorn removal impacts the availability of trace metals in the soil. Increases in Pb and decreases in Cd and Al accompanied all plots where buckthorn was removed regardless of subsequent soil or seeding treatment. Although the elevation of zinc diminished over time, in contrast, the mobilization of lead became more pronounced over time.

This is the first study that shows that buckthorn removal is accompanied by the elevated availability of lead and zinc. Since the methods used evaluate of the relative mobility of soil ions only in the upper layers of the soil, caution is urged in interpreting the results. If this is a general phenomenon, careful study of the fate of lead in the soils of restoration project will need to be undertaken. It may be that this represents a small-scale redistribution of this heavy metal in the superficial layers of the soil. However, if significant lead is mobilized, it will have an adverse impact on subsequent uses of the sites from which buckthorn has been removed.

Reinvasion

Consistent with our expectations, buckthorn seedlings and saplings density was significant reduced in all plots compared with our controls where buckthorn was not cut. Additionally, those plots that had received wood mulch, either of buckthorn or commercial mulch, had lower buckthorn seedling or sapling density than all other treatments. The interpretation of these results is complicated by three factors. First, the reduction in nitrogen is small and not consistent across the two years of our observations. It is therefore unlikely to be a primary factor in influencing buckthorn prevalence. Second, the examination of other soil nutrients showed that the treatments resulted in several significant impacts on the soil environment, some of which may also have had an influence on the revegetation of the plots, but have not been demonstrated in other soil amendment studies that inspired this experimental design. Finally, this experiment focused on employing restoration treatments that managers might reasonably be able to implement. The mulching treatments were therefore incorporated into the soil by rototilling, so these mulching treatments are in fact a compound one constituted by carbon additions and by soil disturbance. Both of these aspects may have had an influence on the plant community.

I make the distinction between buckthorn seedlings and saplings in this study. This distinction is based upon size and the woodiness of small stems, although most measured saplings were very small, typically under 6" tall with a diameter smaller than a pencil. Overlooked, small woody saplings may make an important contribution to the apparent reinvasion of cleared areas. Assuming this to be the case, restoration managers are urged to follow up where which buckthorn has been recently cleared to remove these tiny saplings physically, chemically, or if possible, with prescribed fire. In this study, both seedlings and saplings were reduced in all mulched treatments, but these treatments also included soil disturbance of rototilling to incorporate the mulch into the upper horizon of the soil. Thus, reduction of saplings, in particular, may be as a consequence of tilling the mulch into the soil rather than the presence of the mulch itself (Iannone et al 2013).

Removal of buckthorn from the experimental area increased buckthorn stem density by increasing seedlings and saplings under adult shrubs in the control plots. While this was not an objective of the study, this observation of increased buckthorn density under existing buckthorn thickets, at edges or where the edges have been cleared, suggests that light is a limiting resource for buckthorn establishment and early stages of growth.

Despite lower moisture levels, more buckthorn seedlings germinated and seedlings and saplings grew taller, grew more leaves, and produced more biomass in non-amended soils than those grown in mulch-amended soils. Saplings and seedlings grown in mulch amended soils also showed signs of nutrient stress, yellowing of leaves, and ultimately gained fewer and occasionally lost leaves over time (Figure 13).

Implications for Management

There is a growing appreciation that approaches to restoration that incorporate knowledge of the soil into management practice may be more effective in achieving their stated objectives. This is because the plant community, the diversity of which is often the target of ecological restoration practice, is both influenced by and, in turn, influences soil properties. Since sites with soils having elevated nutrients are often rapidly reinvaded after restoration, the incorporation of soil ecological knowledge (SEK, sensu Heneghan et al. 2008) appears to offer the prospect of improved outcomes. The implications of this study for applying SEK to ecological restoration are several, though none of these are straightforward.

The observation that mulching treatments, the addition of low quality carbon, and its incorporation into the upper layers of the soil reduced the prevalence of buckthorn seedlings and saplings suggests that this may provide a promising approach to restoration in the face of buckthorn. However, the precise mechanism connecting changes to the soil environment to reduced prevalence of the invasive species remain unclear as described above. The changes in the availability soil nitrogen, phosphorus and other nutrients are suggestive, but further work remains to be done before there are clear recommendations for implementing soil amendments in restoration practice. Further, the treatments we used in this experiment involve some fairly pronounced soil disturbances and would therefore have limited application for intact soil which may have a soil structure worth preserving, in addition to this soil being an important source of plant and microbial propagules. Since such soils are increasingly rare, our more radical restoration treatments might, when their impacts are more fully assessed, have broad applicability.

In order to confidently advise for modified management approaches, there needs to be a clearer understanding of the implications of the combinations of simultaneously elevated and reduced soil nutrients for the plant community and for critical ecosystems function.

In most cases where mulched treatments had effects on soil nutrient availability or on buckthorn prevalence, there was no difference between mulch comprising buckthorn woodchips or commercially available mulch. The buckthorn mulch treatment was selected because it is the most abundant source of low quality carbon readily available in areas that may be candidates for restoration. In heavily invaded areas, as was the case of this study site, it may be most economical to remove buckthorn using heavy machinery that leaves ground woody material on the soil surface, rather than hand removal and on-site burning of woody biomass, as is the typical practice in less-densely invaded areas. In areas where there is an existing tree canopy, or areas where the use of heavy machinery is not permitted or feasible, it may not be possible to chip buckthorn material on site. In those instances, bringing woodchips from local municipal tree removals or commercial sources may be the best option. These two different, but common restoration contexts influence this study's design, and the inclusion of store-bought mulch vs buckthorn mulch generated on site. The higher C: N ratio of buckthorn material compared to other woody mulch sources may lead to unexpected impacts on soil nutrient availability compared to lower quality C sources like sawdust, or other woody mulches. However, the use of commercially available mulch may be cost prohibitive for many restoration projects, particularly those lead by volunteers or small conservation organizations and municipalities.

The relative similarity of outcome for both mulch types in this study suggest that either mulch type might further restoration goals, and thus mulch type can be selected as appropriate for each site. However, some response variables differ significantly between the buckthorn and the commercial mulch. This includes the elevation of phosphorus availability in buckthorn mulched treatments. Increased phosphorus availability will also have implications for restoration that merit close attention before wide-scale incorporation of mulch addition following buckthorn removal is implemented.

Synthesis

My dissertation contributes to the field of ecology by examining plants and soils in managed, urban natural areas. Chicago's system of natural areas imbedded in an urban matrix is unique and internationally recognized. The comprehensive network of land managers in the region have been developing, employing, and improving best management practices for restoring terrestrial ecosystems for several decades. While many members of these organizations are actively restoring natural areas and the region has several universities and research institutions conducting ecological research, these two communities have historically not connected in productive or meaningful ways in the long-term. Regionally, there has been no coordinated effort to document, describe, or quantify the impacts of these restoration efforts on plant communities and belowground processes or to provide scientific descriptions of ecosystems that are considered by land managers to be degraded versus those that are high-quality.

In this dissertation, I developed a long-term, landscape-scale, replicated, natural experiment that serves as a framework to investigate the impacts of ecological management practices in the Chicago region and established a baseline for future study. I also investigated alternative restoration techniques that seek to restore processes in conjunction with the native plant community as an example of how soil ecology information can be incorporated into conservation practice.

The Chicago Wilderness Land Management Research Program is more often referred to as the "100 Sites for 100 Years" project, as this nickname quickly conveys the long-term and highly replicated component of the program. The appeal of 100 Sites for 100 Years for graduate students and the value brought to the region in these early establishing years was substantial.

Several young ecologists and new funding opportunities flooded the region's protected spaces with a common mission to better understand the ecology of the region and the efficacy of management efforts. One of the program's greatest strengths is that is satisfies the professional needs of practitioners and researchers. There is a constant flow of students to the region in search of projects, many of whom want to conduct regionally meaningful applied work, but struggle to make the necessary social connections to develop a comprehensive collaborative project. Conservation practitioners and land managers likewise often have questions about the efficacy of certain practices, the feasibility of alternative approaches, and might have experimental designs in mind, but lack the resources to conduct their own studies and often have to react before they are able to collect baseline or control data.

Without a champion, this momentum has faded. Greater involvement could and should be reinvigorated within the next few years. The existing network of sites and collaborating institutions could also be expanded to include more urban habitats and partners and would require minimal financial support. This expansion and continuation would not only be a valuable resource for ecologists and managers in the region, but would also contribute to the field of ecology by providing a greater quantity and quality of studies focused on the similarities and differences in ecosystems where humans are a critical and regular component.

In the absence of on-going support, the data collected and described in this dissertation and subsequent publications can be referenced in a few years or several decades. This re-examination could explore ecological questions with a longer temporal lens. For example, questions regarding the impacts of climate change on certain species, or this data could provide a reference for success in restoring oaks in the region. The baseline data could also be used to explore species interactions that may emerge in 50 years and the data collected here may provide a critical historical reference. Whether the approach is comparative or experimental, a long-term perspective is critical to developing our understanding of a broad suite of ecological phenomena and processes. Documenting and forecasting ecological change, particularly in relationship to activate land management, requires an understanding of interactions of spatial and temporal dynamics of ecological systems, necessitating studies at multiple scales. The 100 Sites for 100 Years program, like LTER sites, is intentionally and uniquely set up for these investigations.

The links between aboveground focused management efforts and belowground processes remains one of ecology's less explored fields. Rarely are soil nutrients or biotic components of an ecosystem assessed prior to, during, or following restoration activities. This omission may have significant consequences for restoration outcomes in terms of establishing a target plant community or the ecological processes that sustain said community. Relationships between invasive plants and soil nutrient availability is well established in the literature, but not regularly addressed in practice. While managers generally recognize the importance of soil conditions, they often lack the facilities to explore these relationships. Even when resources to test hypotheses there is a lack of clear, implementable methods to apply to altered conditions. For example, in Chapters 2 & 4, I demonstrate that prairie restorations have elevated soil phosphorus compared to remnants and suggest that this difference likely influences community composition and above-belowground interactions. Managers could investigate the soil phosphorus levels on the site that they are managing, but this level of investigation lacks purpose if there is no proposed alternative management practice that addresses said elevated phosphorus levels.

Understanding the impacts of both historical land use and current management practices on critical ecological processes can help guide future land conservation and management practices to ensure long term sustainability of natural areas. In prairies, the legacy effect of row-crop agriculture is profound and appears to impact ecosystems for decades thereafter. Elevated soil phosphorus, a likely symptom of over fertilization and/or the use of slow-release fertilizers, can influence plant community establishment and the interactions between plant roots and soil organisms, particularly mycorrhizal fungi. If a primary goal or prairie restoration is to restore a biologically diverse, resilient ecosystem, the long-term impacts of historical land-use must be addressed by ecologists in a way that describes the symptoms and provides hypothesized approaches to ameliorate those concerns.

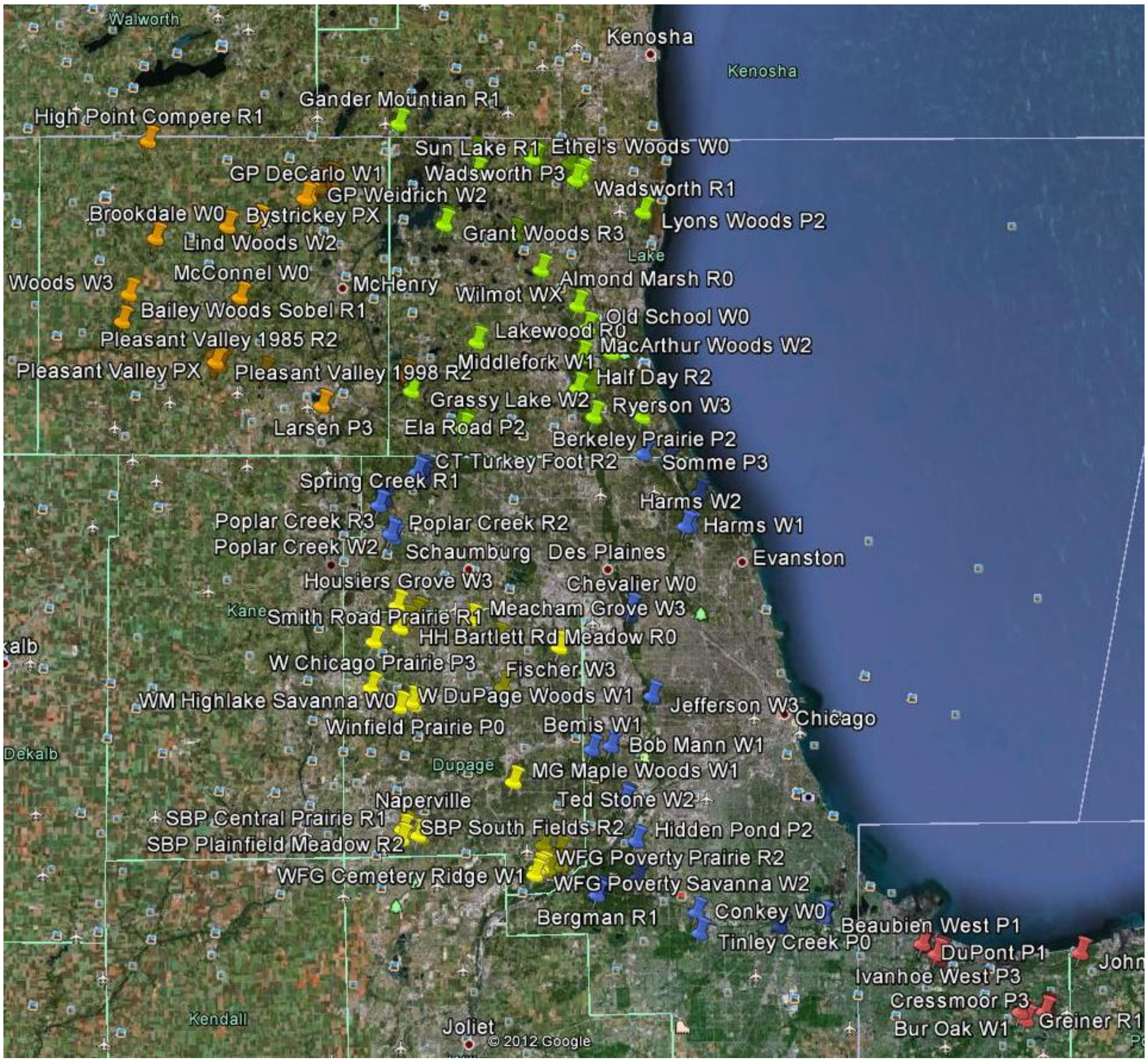
In woodlands, soil N and earthworm biomass should be considered alongside buckthorn density, habitat context, and other social and political factors prior to initiating restoration. I hypothesize that low levels of one or more of these factors will lead to better restoration outcomes – restoration of herbaceous native plant community – with lower resource commitment. Once buckthorn or other invasive shrubs are removed, follow-up treatment of tiny saplings that were missed during clearing, through mechanical methods (tilling), burning, or repeated mowing is essential.

Current hypotheses of plant invasion, including the driver and passenger models and the more recent back seat driver model suggest that invasive species success coincides with altered ecosystem functions and that simple removal of the exotic species will not result in restoration of biologically diverse, ecologically functioning natural area. Areas invaded by non-native invasive plants and those formerly used for agricultural production are associated with high soil nutrient levels, altered soil faunal communities and decomposition rates; and these effects are thought to persist following invasive plant removal, thereby hindering the successful restoration of native plant. Elevated soil nutrients can contribute to an area's susceptibility to plant invasion and/or domination by rapidly growing, weedy species at the expense of slower growing, native species and this condition can persist following restoration. In the last chapter, I investigated alternative methods to restoration that addresses these relationships and links the earlier descriptive chapters in a manipulative experiment.

In this dissertation, I aimed to provide a sympathetic, but quantifiable examination of the efficacy of regional conservation efforts. After years of field and lab work, traveling throughout the region, I recommend that on-going management of remnants should remain the highest priority followed by the on-going management of restorations. Reinvasion is pervasive in all ecosystems, and continued and consistent maintenance is essential to achieve regional biodiversity and conservation goals.

When selecting new areas for restoration, a comprehensive site assessment should be conducted and should include basic soil nutrient availability analysis along with an assessment of the floral and faunal community. Restoration goals should also be clearly defined so that they can be properly evaluated. In some cases, restoration goals may focus on a target species. In others, goals may be more general, referring to a theoretical ecological target. Managers often have a mental vision of this target, represented by a particularly diverse, aesthetic, or other subjectively preferred reference site. These sites might be favorites for practitioners, and while they may be useful sites for inspiration or inquiry, they may not be realistic or appropriate ecological targets in highly urbanized areas.

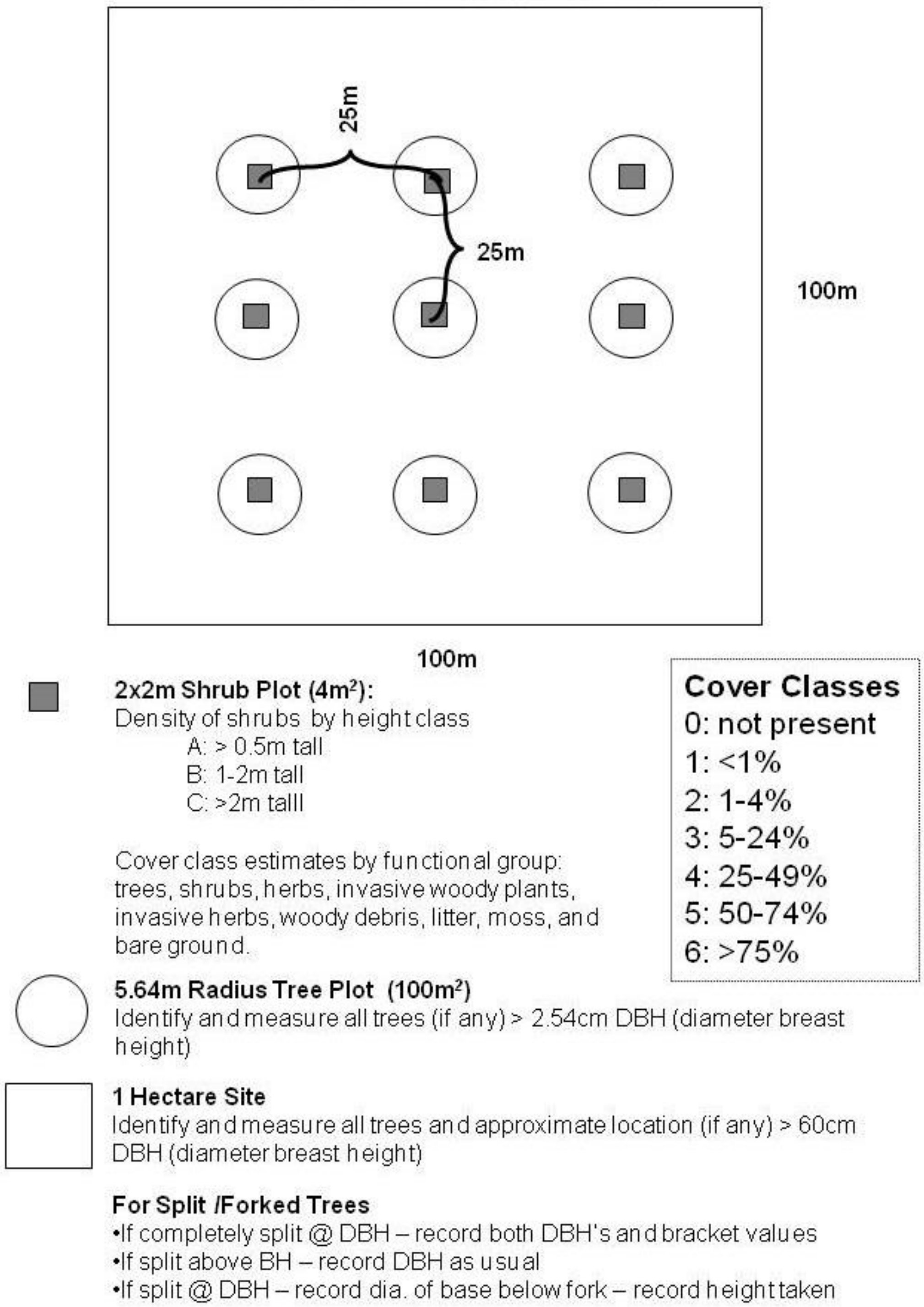
Tables and Figures



Ch1. Figure 1: Google earth image of entire network of 121 sites color coded by county with site name and abbreviations.

Ch1. Table 1: Study sites by habitat and management category, and number of sites in each category.

Management Category	**Woodlands**	**Prairie Restorations**	**Prairie Remnants**
Degraded/Control/Unmanaged	**13**	**7**	**4**
Early Management (<10yrs)	**14**	**14**	**6**
Intermediate Management (>10yrs)	**13**	**13**	**11**
Reference (also managed)	**7**	**4**	**10**
Unique (uncategorized)	**2**	**0**	**3**



Ch1. Figure 2: Layout of vegetation sampling plot within each study site.

Ch1. Figure 3: Tree canopy photo taken at breast height (1.4m) after processing through GLA 2.0.

Ch1. Figure 4: PRS probe arrangement. Two sets of two cation (purple) and two anion (orange) probes were installed 5 m from the center point of each plot.

Ch2. Table 1: Woodland vegetation summary by management category. Values given as median/mode etc. n is the number of sites.

	Control/Unmanaged n=12				Early Management n=13				Intermediate Management n=12				Reference n=7				Unique n=2			
	Average	*SE*	*Median*	*Mode*	*Average*	*SE*	*Median*	*Mode*	*Average*	*SE*	*Median*	*Mode*	*Average*	*SE*	*Median*	*Mode*	*Average*	*SE*	*Median*	*Mode*
Bareground	2.19	0.254	2	2	2.14	0.470	2	1	1.92	0.447	2	2	2.32	0.529	2	3	3.11	1.304	3	1
Leaf Litter	5.12	0.396	6	6	4.18	0.495	4	6	4.23	0.515	5	6	4.35	0.645	5	6	4.89	0.836	5	6
Moss	0.56	0.263	0	0	0.48	0.254	0	0	0.63	0.317	0	0	0.35	0.273	0	0	0.33	0.542	0	0
Woody Debris	3.08	0.198	3	3	2.81	0.323	3	3	2.49	0.345	2	2	3.24	0.411	3	3	2.83	0.813	3	3
Herbaceous	2.78	0.454	3	3	4.43	0.417	5	6	4.73	0.348	5	6	4.24	0.483	4	3	3.50	1.007	4	2
Shrubs	2.69	0.490	3	3	1.86	0.499	2	0	2.07	0.525	2	0	2.05	0.732	2	0	1.17	1.036	0.5	0
Tree	0.82	0.344	0	0	0.54	0.271	0	0	0.61	0.305	0	0	0.44	0.331	0	0	0.77	1.044	0	0
Invasive Woody	2.91	0.456	3	3	1.72	0.472	1	0	2.08	0.480	2	0	0.40	0.350	0	0	2.17	0.849	2	1
Invasive Herbaceous	1.34	0.517	0	0	1.49	0.467	1	0	1.42	0.511	0	0	1.11	0.596	0	0	1.06	0.856	1	1

Ch2. Table 2: Vegetation summary of all prairies using median cover class for each site. N is the number of sites in each management category.

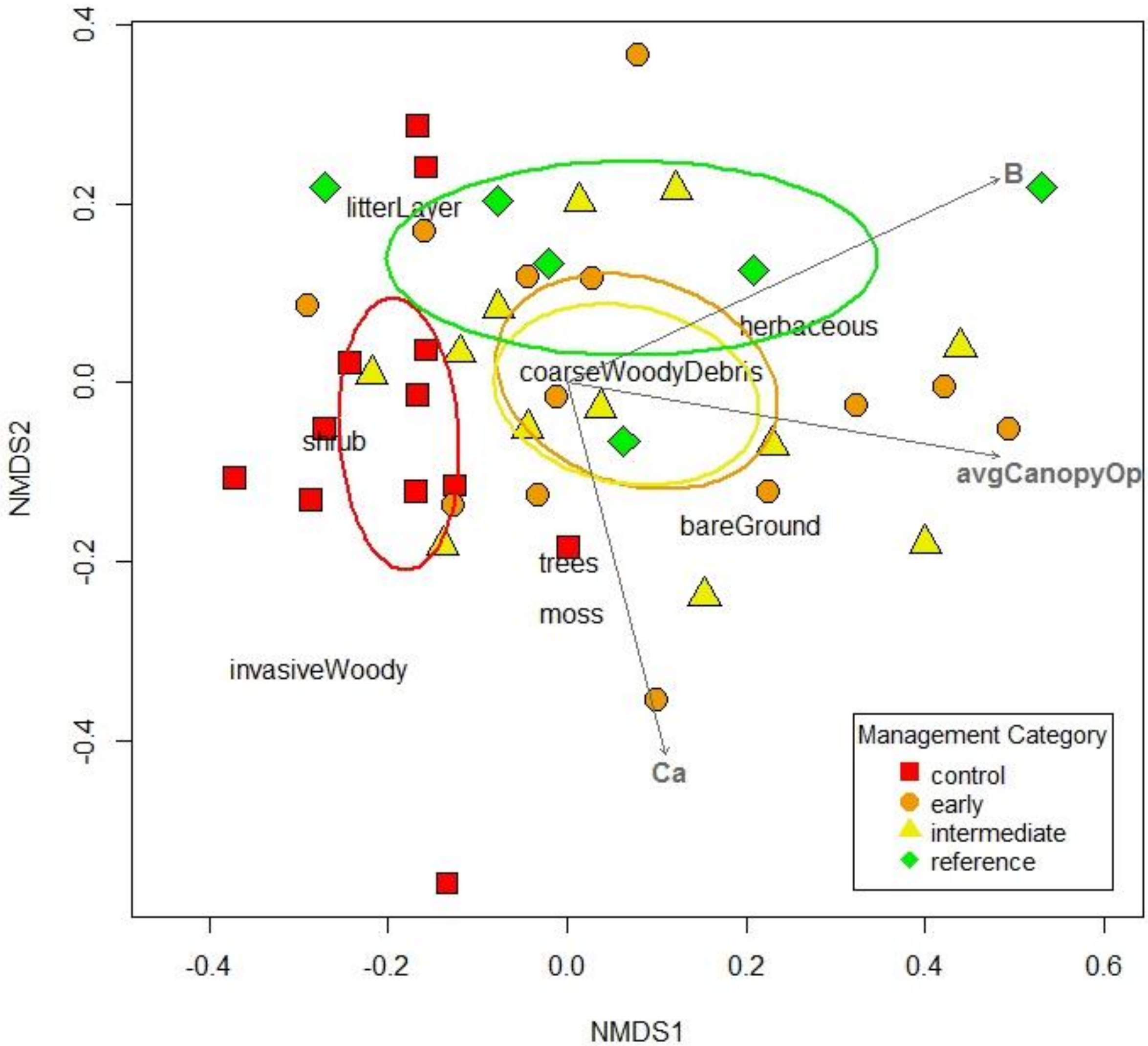
	Control/Unmanaged				**Early Management**				**Intermediate Management**				**Reference**				
	n=12				n=13				n=12				n=7				
	Average	*SE*	*Median*	*Mode*	*Average*	*SE*	*Median*	*Mode*	*Average*	*SE*	*Median*	*Mode*	*Average*	*SE*	*Median*	*Mode*	*Average*
Bareground	2.19	0.254	2	2	2.14	0.470	2	1	1.92	0.447	2	2	2.32	0.529	2	3	3.11
Leaf Litter	5.12	0.396	6	6	4.18	0.495	4	6	4.23	0.515	5	6	4.35	0.645	5	6	4.89
Moss	0.56	0.263	0	0	0.48	0.254	0	0	0.63	0.317	0	0	0.35	0.273	0	0	0.33
Woody Debris	3.08	0.198	3	3	2.81	0.323	3	3	2.49	0.345	2	2	3.24	0.411	3	3	2.83
Herbaceous	2.78	0.454	3	3	4.43	0.417	5	6	4.73	0.348	5	6	4.24	0.483	4	3	3.50
Shrubs	2.69	0.490	3	3	1.86	0.499	2	0	2.07	0.525	2	0	2.05	0.732	2	0	1.17
Tree	0.82	0.344	0	0	0.54	0.271	0	0	0.61	0.305	0	0	0.44	0.331	0	0	0.77
Invasive Woody	2.91	0.456	3	3	1.72	0.472	1	0	2.08	0.480	2	0	0.40	0.350	0	0	2.17
Invasive Herbaceous	1.34	0.517	0	0	1.49	0.467	1	0	1.42	0.511	0	0	1.11	0.596	0	0	1.06

Ch2. Table 3: Summary of woodland soil moisture, select soil macronutrient availability, total carbon, total nitrogen, carbon to nitrogen ratio, and canopy openness according to management category and results from Kruskal-Wallis tests. Significantly different results are in italics and bold. Units for soil nutrients are µg/cm^3/28days. % Carbon, % Nitrogen are percent by dry weight.

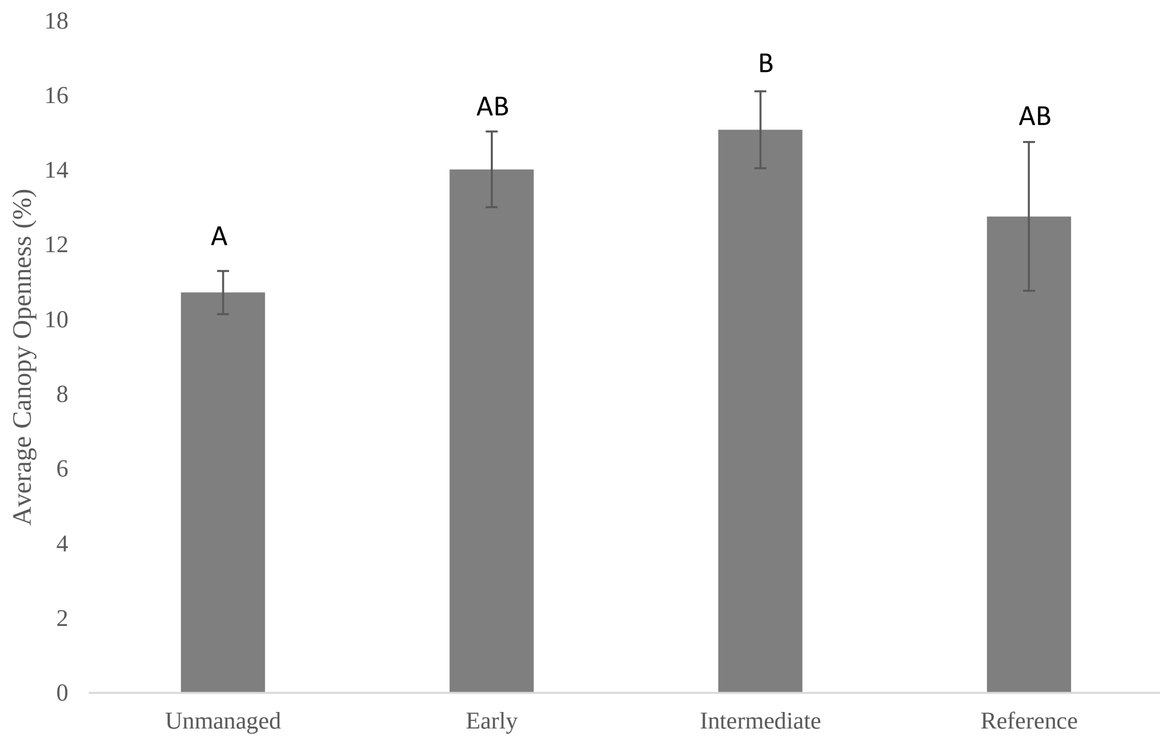
	Control n= 12		**Early** n=13		**Intermediate** n=12		**Reference** n=7		**Management**	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	χ2	p
% Moisture	0.29	0.05	0.27	0.01	0.25	0.032	0.20	0.03	2.81	0.42
Total N	189.9	65.9	57.1	15.4	56.5	24.8	33.3	7.6	2.64	0.45
NO3	184.4	64.9	51.4	16	51.3	25.4	30.8	7.5	3.03	0.39
NH4	5.5	2	5.7	1.3	5.1	1.2	2.5	0.3	3.66	0.30
P	4.6	1.3	3.5	0.6	6.9	1.4	3.7	0.7	3.23	0.36
K	61	9.2	68.9	12.6	56.7	11.4	55.4	9.7	1.12	0.77
Ca	1824	146	1857	150.5	2066	174	1827	162.7	1.15	0.76
B	0.97	0.2	1.5	0.2	1.5	0.3	1.4	0.29	3.65	0.3
% Carbon	4.38	0.62	5.12	0.59	4.75	0.98	4.62	0.4	3.23	0.36
% Nitrogen	0.37	0.05	0.41	0.05	0.39	0.07	0.35	0.04	1.42	0.7
C: N	12.2	0.6	12.8	0.6	12.2	0.4	13.4	0.6	2.81	0.42
% Canopy Openness	10.7	0.58	14.02	1.0	15.08	1.0	12.76	2.0	***12.9***	***0.005***

Ch2. Table 4: Summary of all prairie remnant and restoration soil moisture, select soil macronutrient availability, total carbon, total nitrogen, and carbon to nitrogen ratio, according to management category and results from Kruskal-Wallis tests for differences by land-use history and management category. Soil nutrients are in µg/cm^3/28 days. Carbon (% C) and Nitrogen (% N) are percent by dry weight. Significantly different results are in italics and bold.

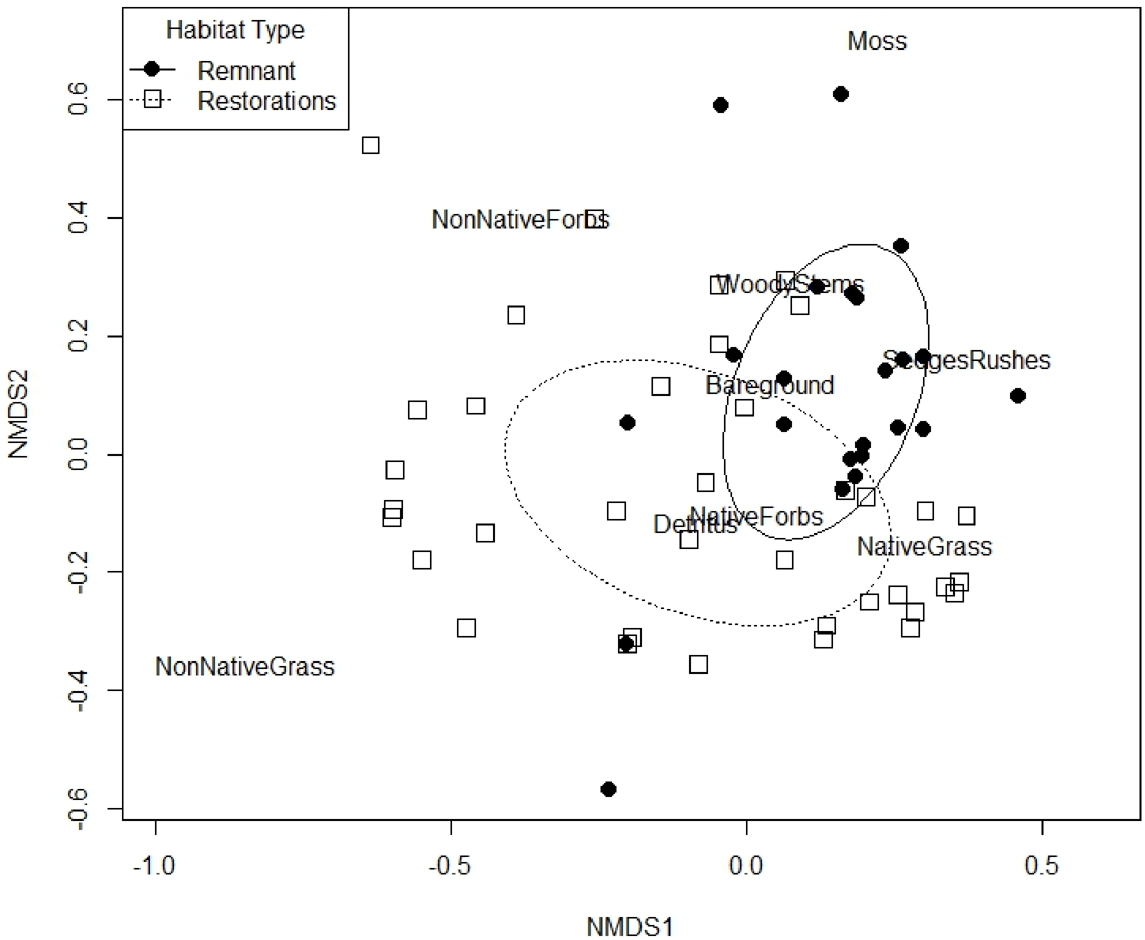
	Control		**Early**		**Intermediate**		**Reference**		**Land-Use History**		**Management**	
	n= 12		n=17		n=23		n=8					
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	$\chi 2$	p	$\chi 2$	p
% Moisture	0.18	0.02	0.22	0.04	0.19	0.02	0.23	0.07	0.07	0.79	0.03	1
Total N	10.83	1.14	13.52	3.22	17.3	6.34	9.43	2.16	0.83	0.36	3.6	0.31
NO3	7.58	0.98	9.67	3.28	13.96	6.35	4.94	1.23	0.63	0.43	3.97	0.26
NH4	3.26	0.32	3.85	0.45	3.33	0.47	4.49	1.84	<.001	0.98	1.87	0.60
P	9.75	2.92	9.26	2.40	9.89	2.12	10.93	4.92	***16.6***	***<0.001***	0.11	0.99
K	61.13	10.8	58.36	11.7	64.64	8.92	49.96	17.82	0.39	0.53	1.79	0.62
Ca	2055.7	49.8	2245.3	94.3	2029.6	101.6	2456.8	273.2	0.31	0.58	6.51	0.09
% C	4.81	0.38	5.13	0.56	5.39	1.11	5.32	1.07	0.87	0.35	1.06	0.79
% N	0.40	0.03	0.39	0.04	0.48	0.13	0.44	0.10	2.42	0.12	0.46	0.93
C: N	12.22	0.39	13.53	1.21	12.09	0.40	12.32	0.54	0.57	0.45	1.53	0.67



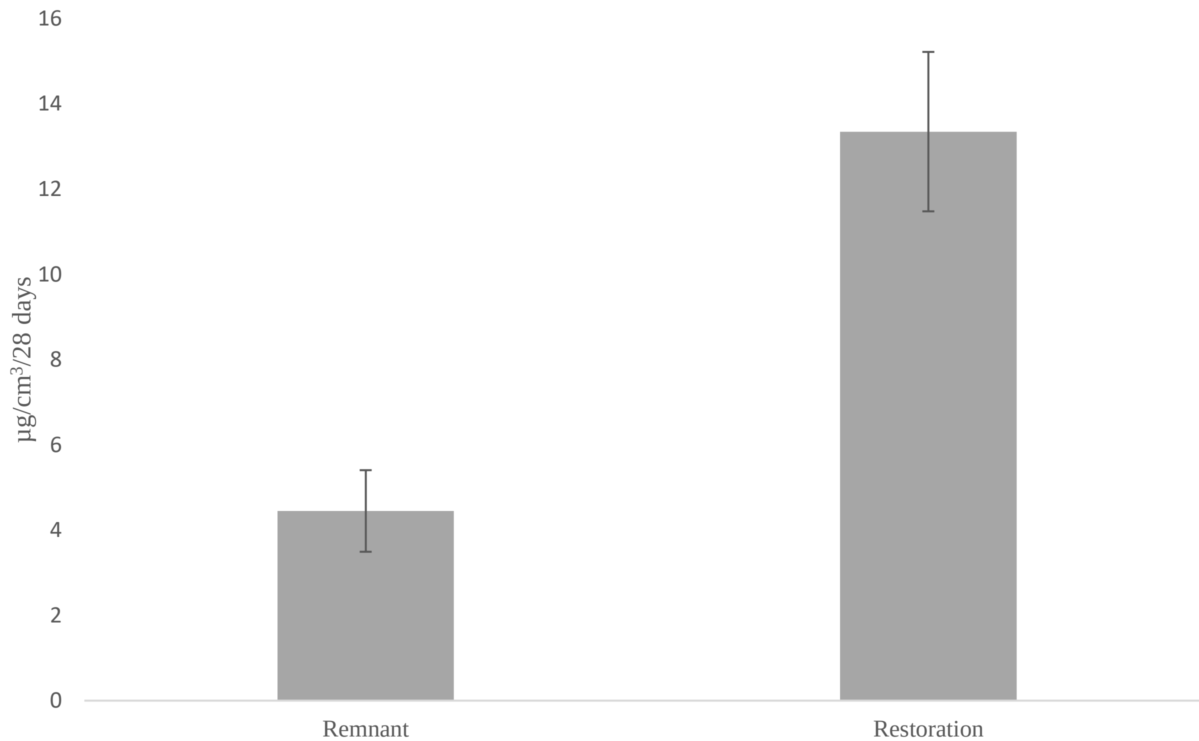
Ch2. Figure 1: NMDS showing relationships of median functional plant group cover by management category in woodlands. Each point represents a site and is symbolized according to management category color coded along a green to red color scale. Green diamonds are reference sites, yellow triangles are intermediate sites, orange circles are early management sites, and red squares are unmanaged sites. Ellipses of the corresponding color represent standard deviations that management category. Functional plant groups are plotted on the figure as they relate to the ordination.. Permanova results indicate significant differences in plant community by management category ($R^2 = 0.097$, $p = 0.005$). Ordination stress = 0.18; ordination distance-observed dissimilarity, $R^2 = 0.97$ non-metric fit; $R^2 = 0.85$ linear fit. Significant soil variables are plotted as vectors ($p < 0.05$).



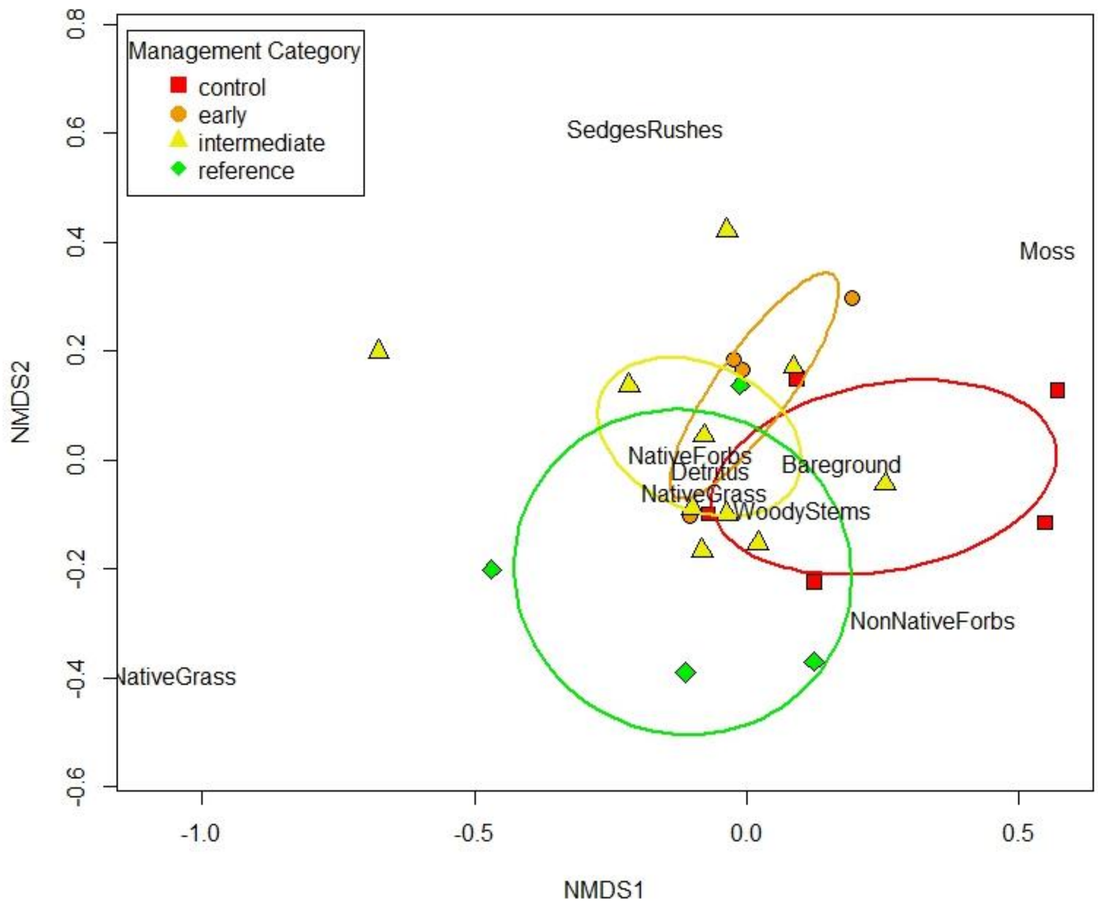
Ch2. Figure 2: Average canopy openness by management category. Difference letters indicate significant differences between canopy openness.



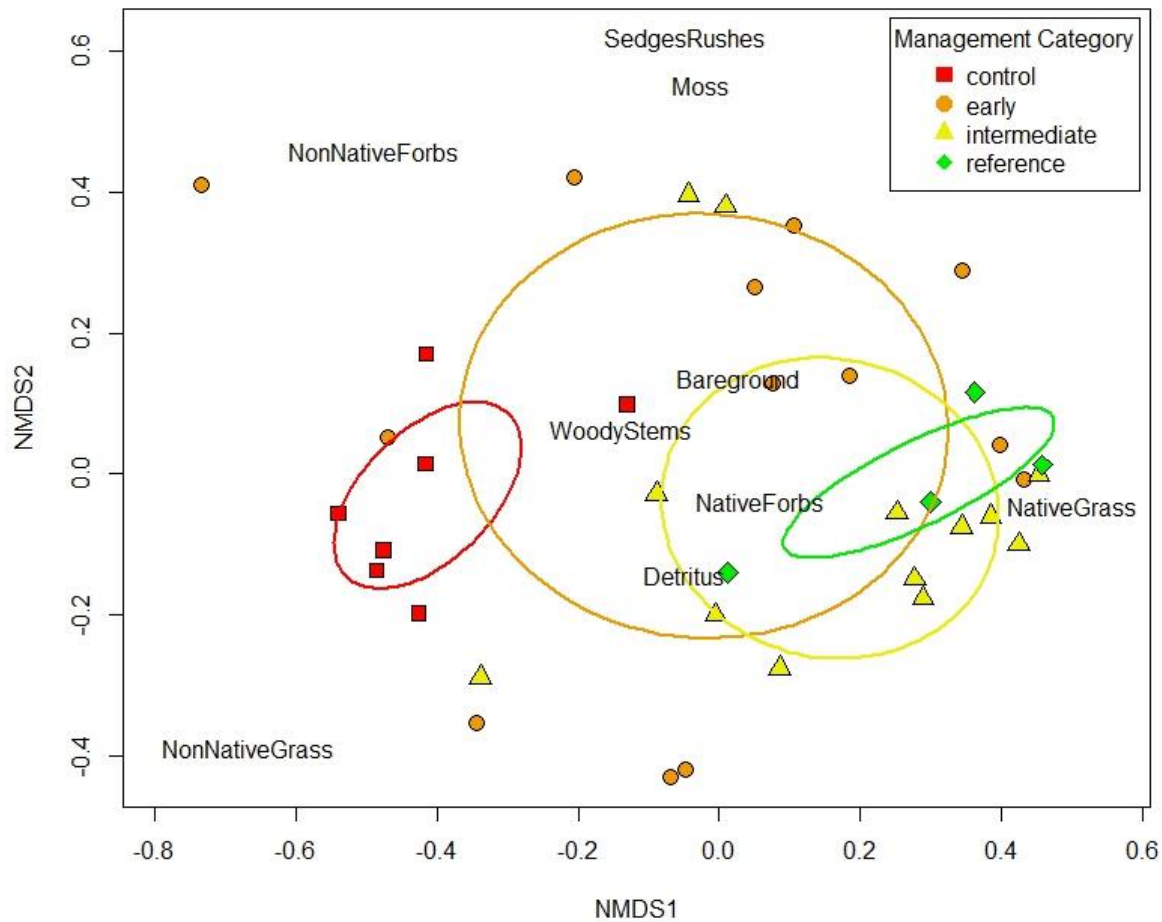
Ch2. Figure 3: NMDS of median functional plant group cover by prairie land use history. Each point represents a site labeled according to land use history and plant functional groups are plotted. Ellipses represent the standard deviations that land use history type. Permanova results indicate that plant community structure differs significantly by land-use history (R^2 = 0.06, p < 0.001). Stress = 0.13 with strong correlation between ordination distance and observed dissimilarity, R^2 = 0.96 for non-metric fit and R^2 = 0.83 for linear fit.



Ch2. Figure 4: Soil phosphorus availability by land-use history in prairies. Asterisk indicates significant different between the two land-use history categories ($p = 0.002$).



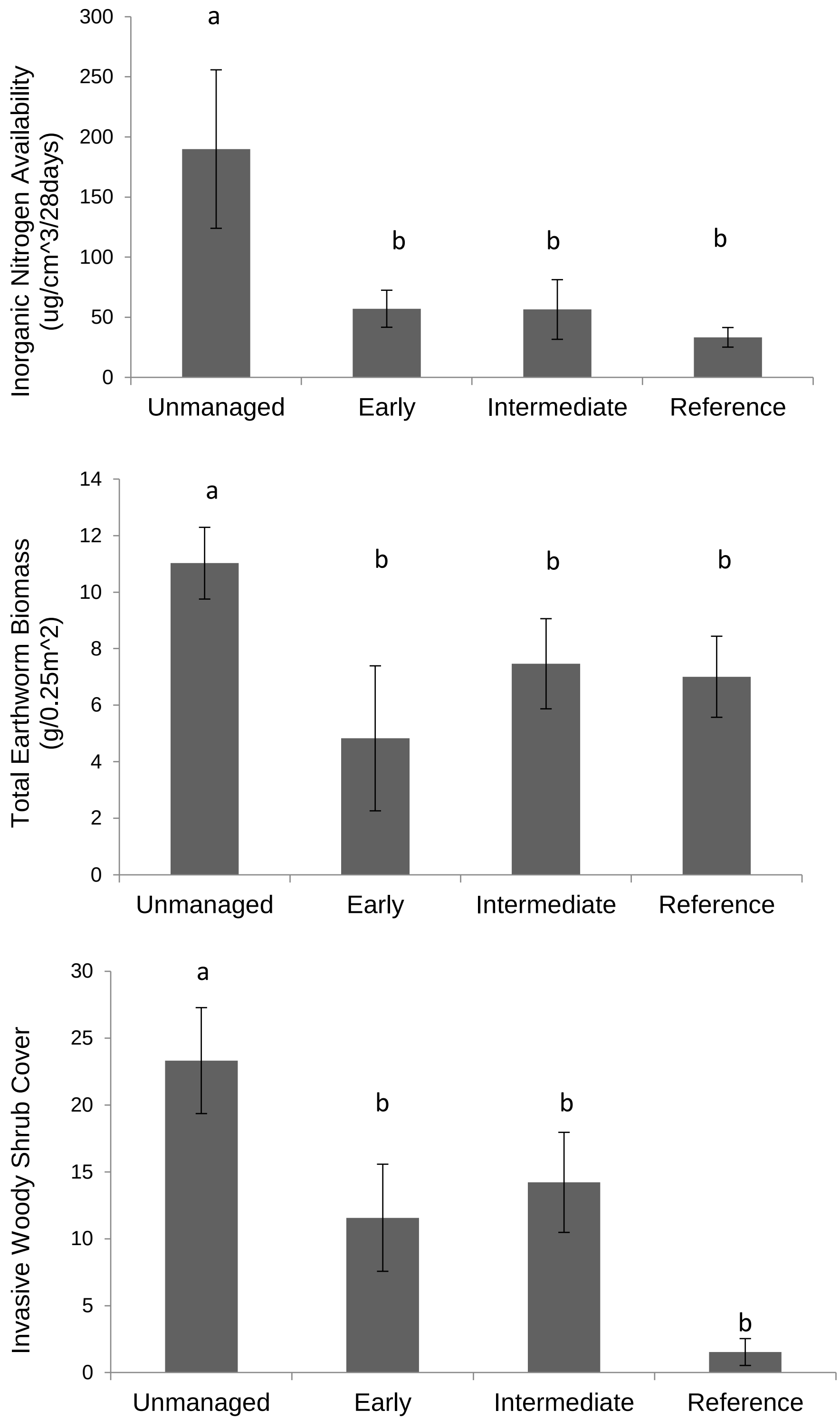
Ch2. Figure 5: NMDS of functional plant group cover of prairie remnants by management category. Each point represents a site and is symbolized according to management category color coded along a green to red color scale. Green diamonds are reference sites, yellow triangles are intermediate sites, orange circles are early management sites, and red squares are unmanaged sites. Ellipses of the corresponding color represent standard deviations that management category. Functional plant groups are plotted on the figure as they relate to the ordination. Permanova indicates that plant communities differ by management (R^2 = 0.14, p = 0.001) and county (R^2 = 0.17, p = 0.03). Ordination stress = 0.17, non-metric fit R^2 = 0.971, linear fit R^2 = 0.89.



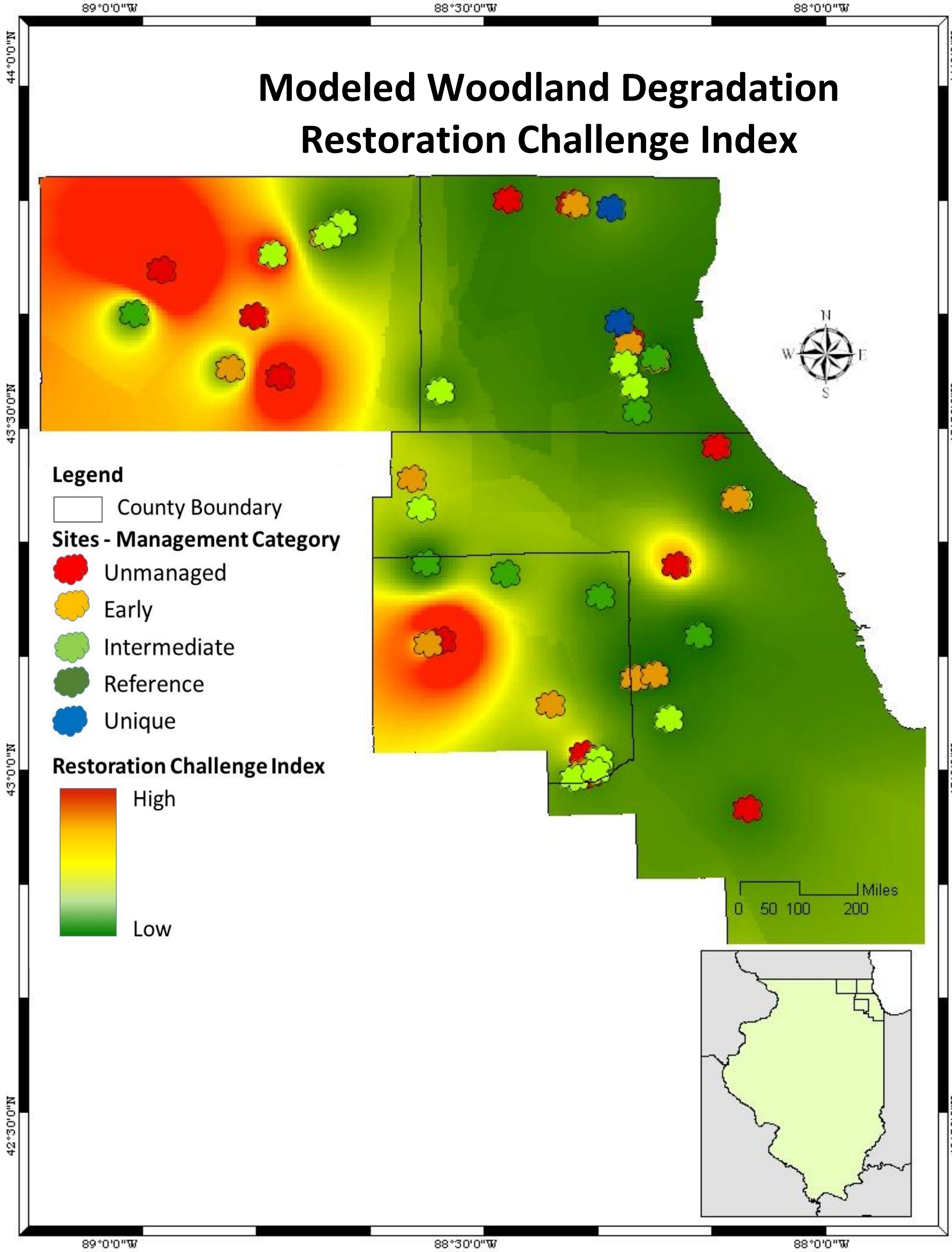
Ch2. Figure 6: NMDS of functional plant group cover in prairie restorations by management category. Each point represents a site and is symbolized according to management category color coded along a green to red color scale. Green diamonds are reference sites, yellow triangles are intermediate sites, orange circles are early management sites, and red squares are unmanaged sites. Ellipses of the corresponding color represent standard deviations that management category. Functional plant groups are plotted on the figure as they relate to the ordination. Permanova results indicate that vegetation differs by management type (R^2 = 0.22, $p < 0.001$). Ordination stress = 0.16, non-metric fit R^2 = 0.975, linear fit R^2 = 0.88.

Ch3. Table 1: Descriptions of management categories and site replicates.

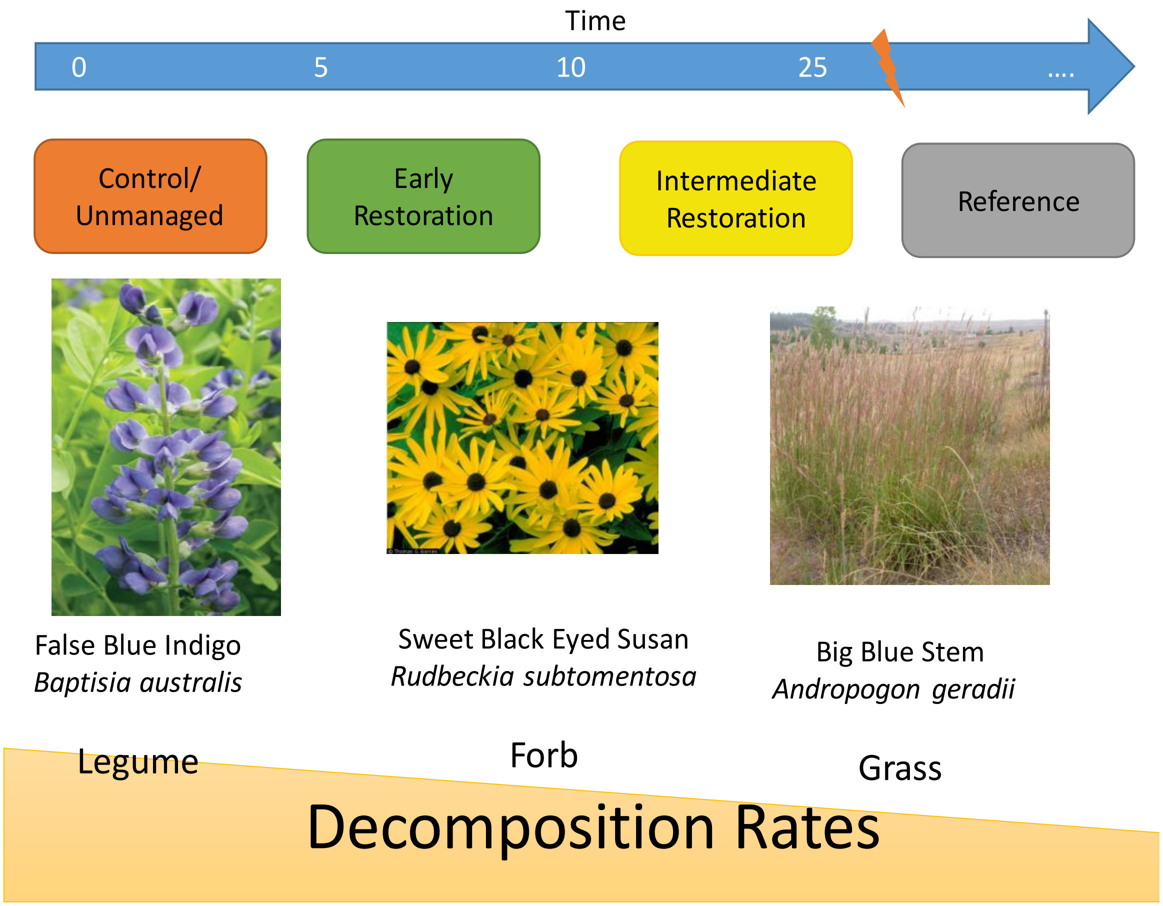
Management Category (# sites)	**Description**
Unmanaged (n= 12)	Unmanaged woodland, considered degraded by managers
Early Restoration (n = 13)	Managed for < 10 years
Intermediate Restoration (n=12)	Managed for > 10 years
Reference (n=7)	Managed, high quality reference woodland



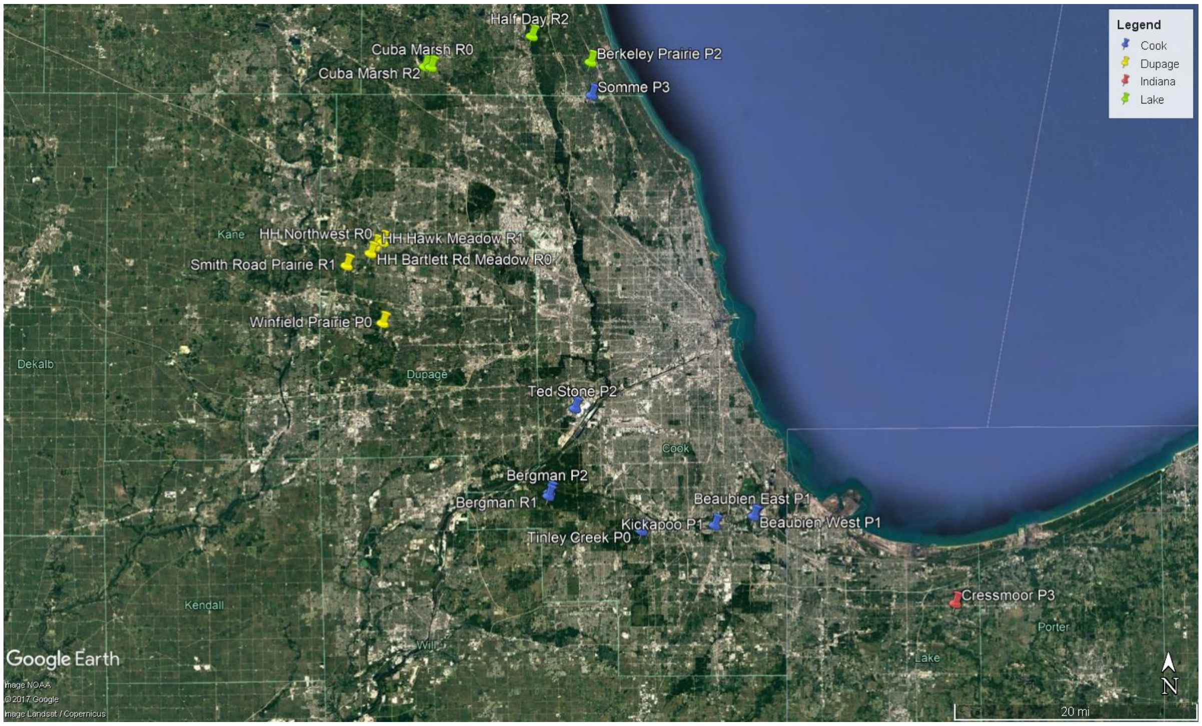
Ch3. Figure 1: Mean total inorganic N availability (a) mean total earthworm biomass (b) and invasive woody shrub cover (c) by management category. Vertical bars indicate the standard error of the mean. Different letters indicate statically significant differences ($p < 0.05$).



Ch3. Figure 2: Modeled potential degradation or restoration challenge index of natural areas throughout Cook, DuPage, Lake and McHenry counties in Illinois. Model is generated as a product of inverse distance weight squared spatial interpolation raster files of sampled woodland earthworm biomass, soil nitrogen availability and invasive shrub cover at 44 woodland sites.

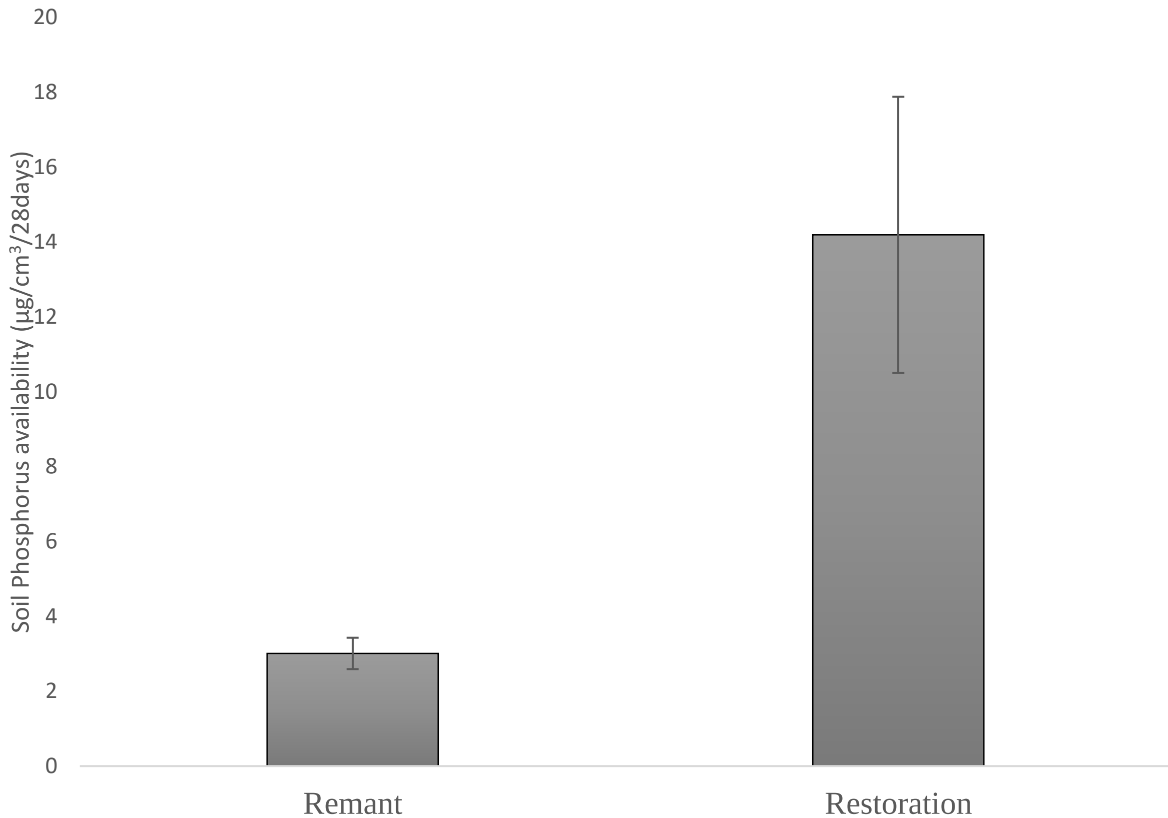


Ch4. Figure 1: Conceptual mode of experiment.

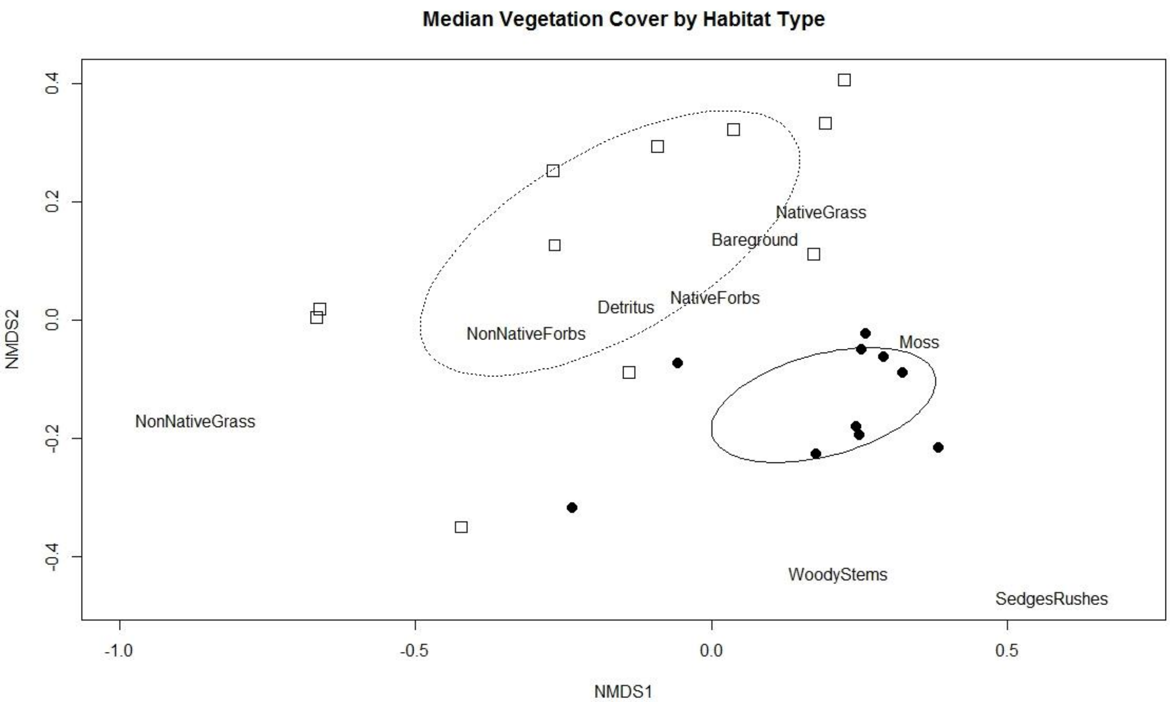


Ch4. Figure 2: Map of study sites.

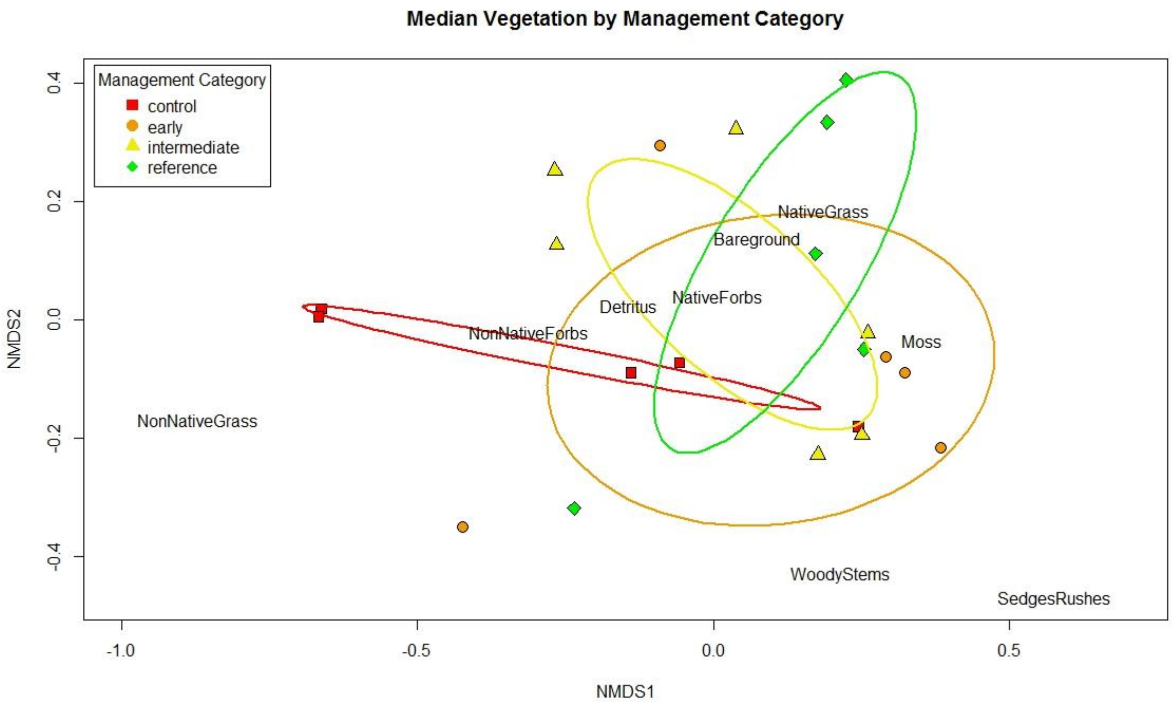
Ch4. Figure 3: Litter bag installation.



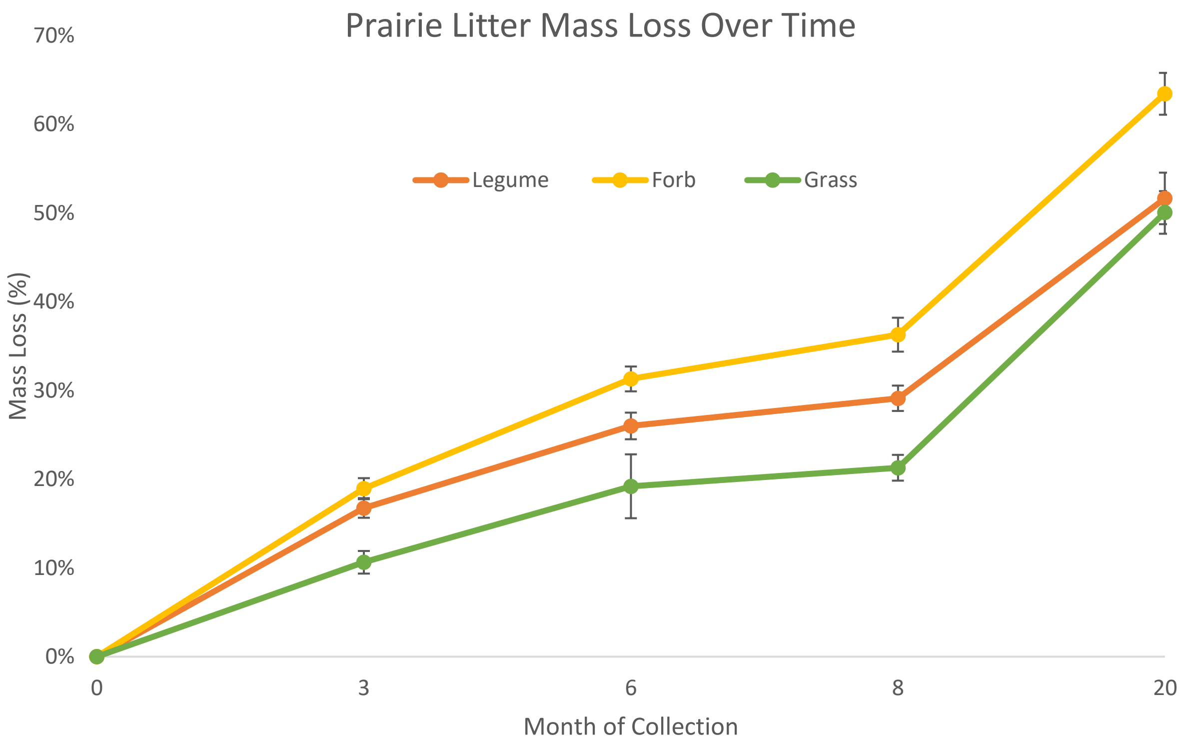
Ch4. Figure 4: Soil Phosphorus availability is significantly higher in prairie restorations compared to remnants (p=0.0098, F=8.234).



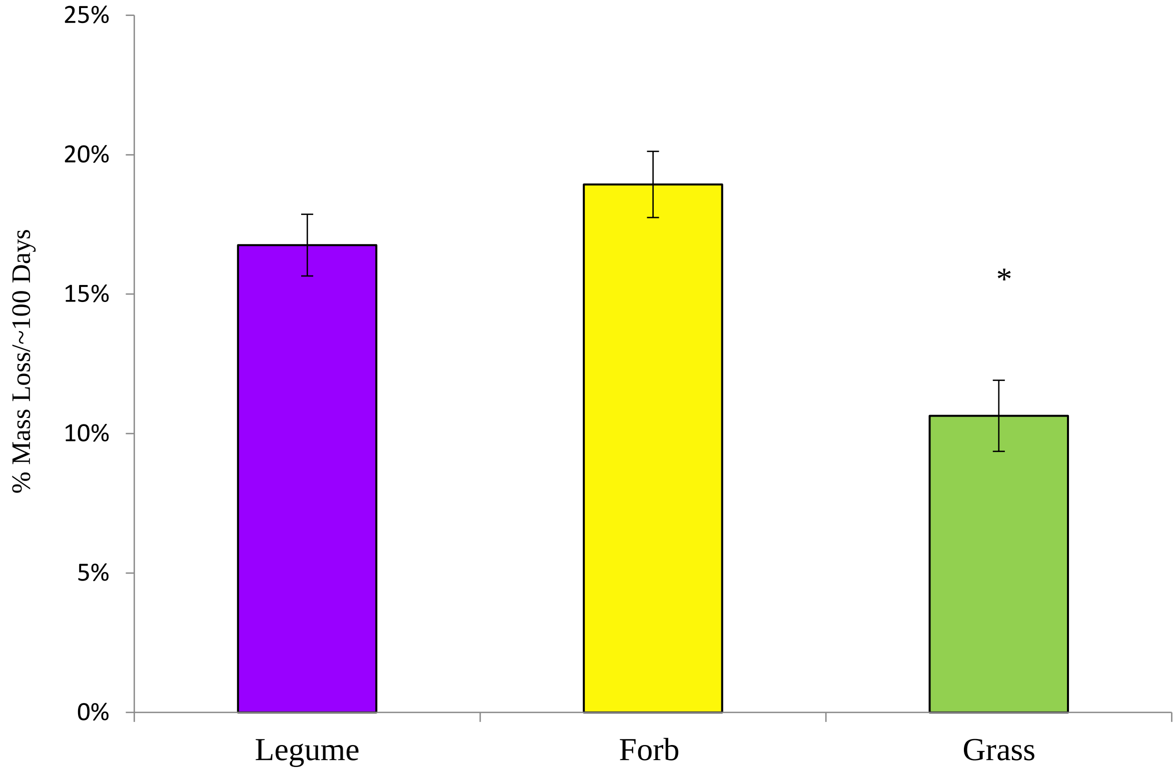
Ch4. Figure 5: Median vegetation cover by habitat type.



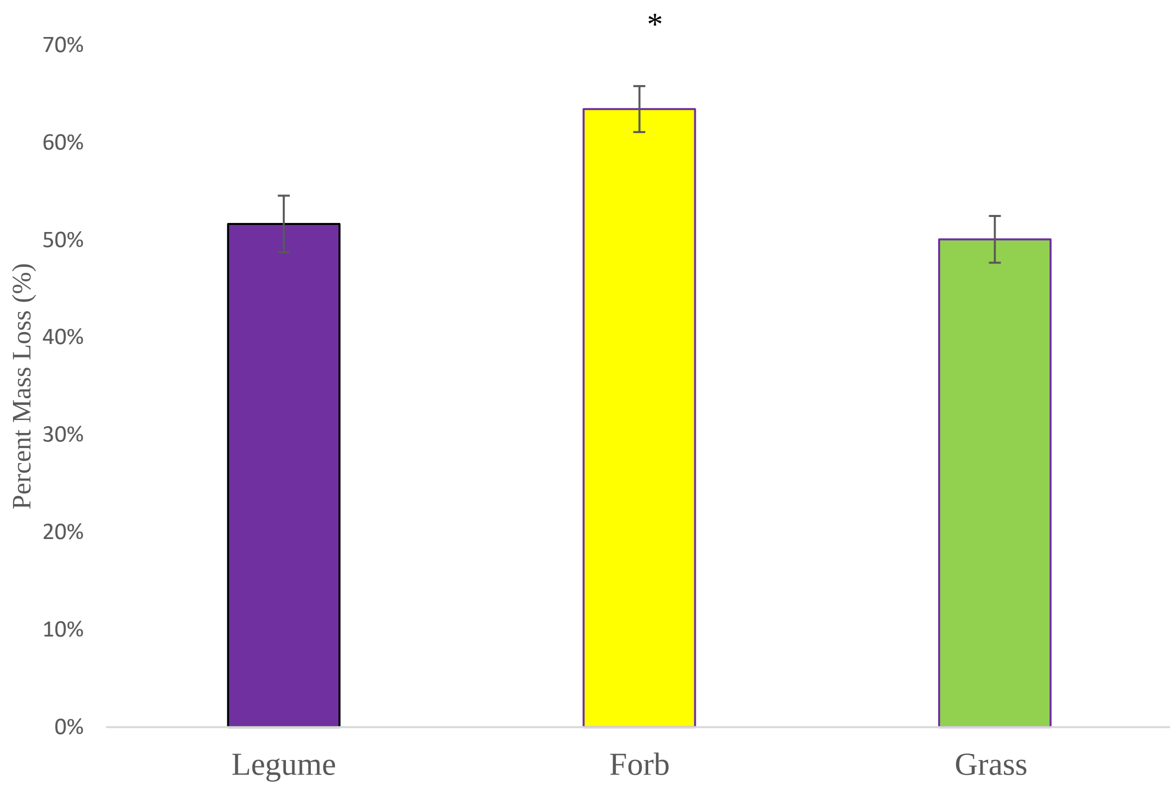
Ch4. Figure 6: Median vegetation cover by management category.



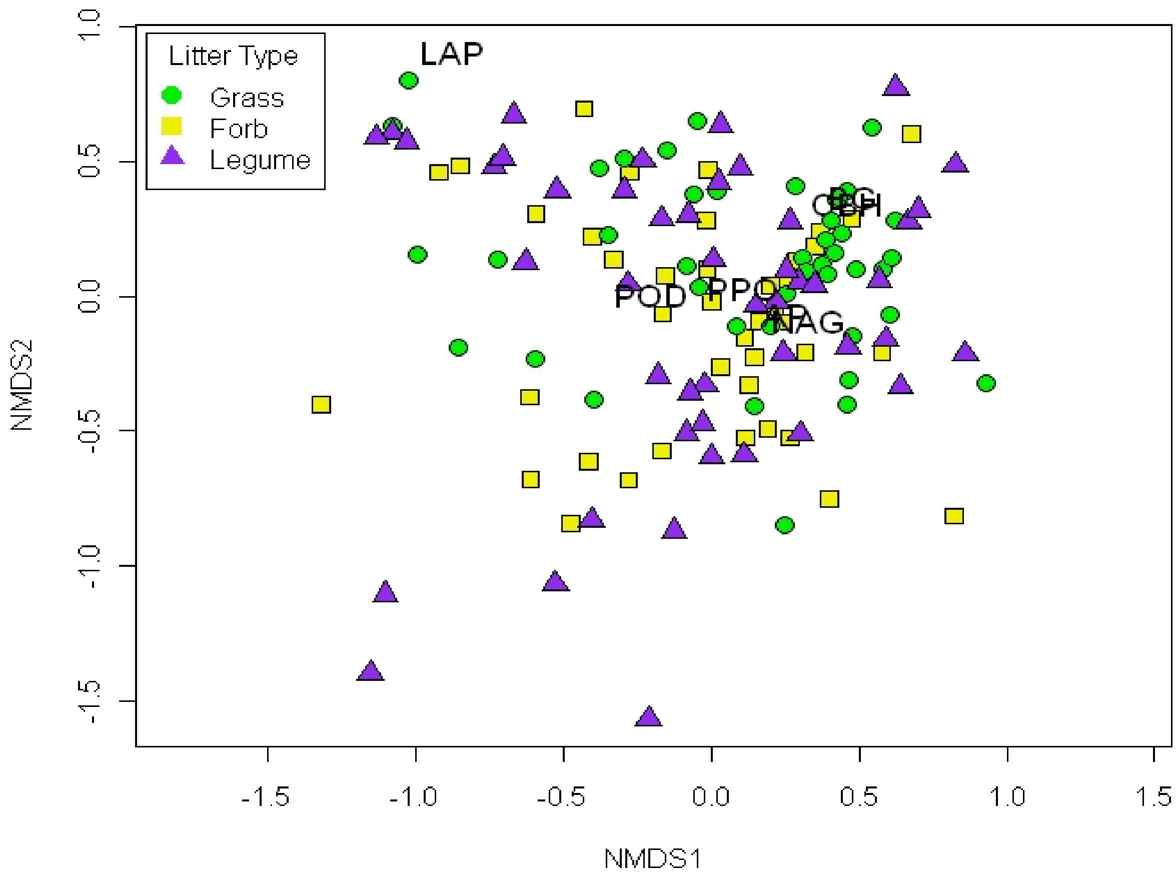
Ch4. Figure 7: Lead litter mass loss over time.



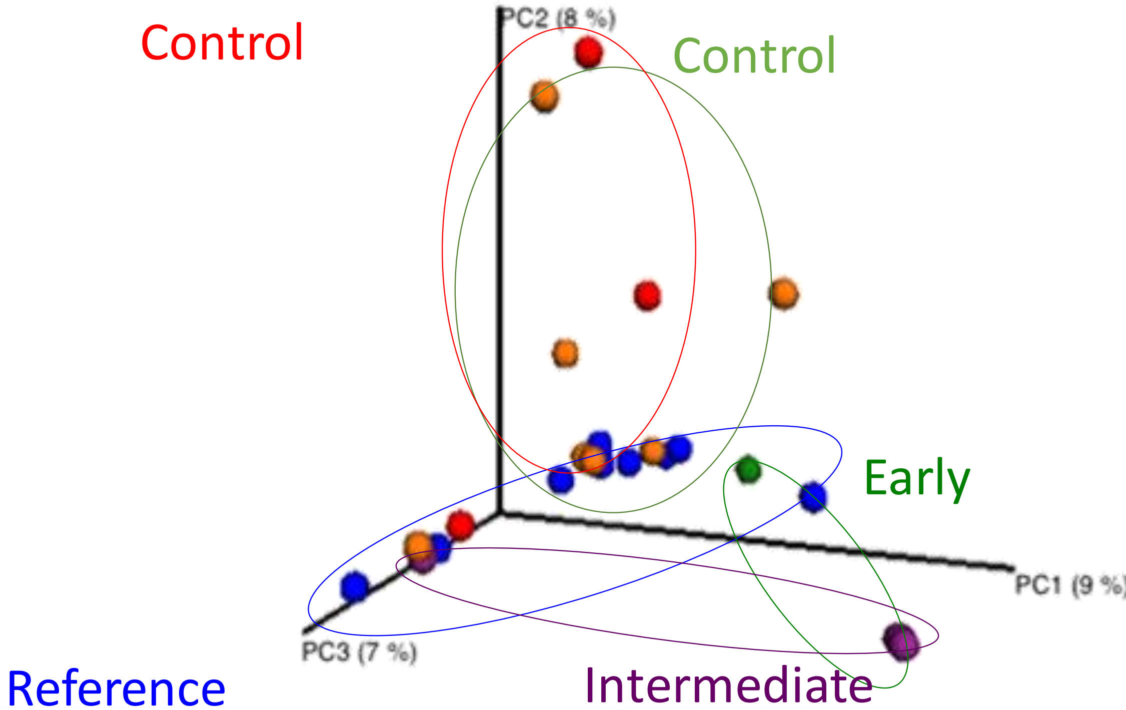
Ch4. Figure 8: Mass loss by litter type for collection 1 (June 2013).



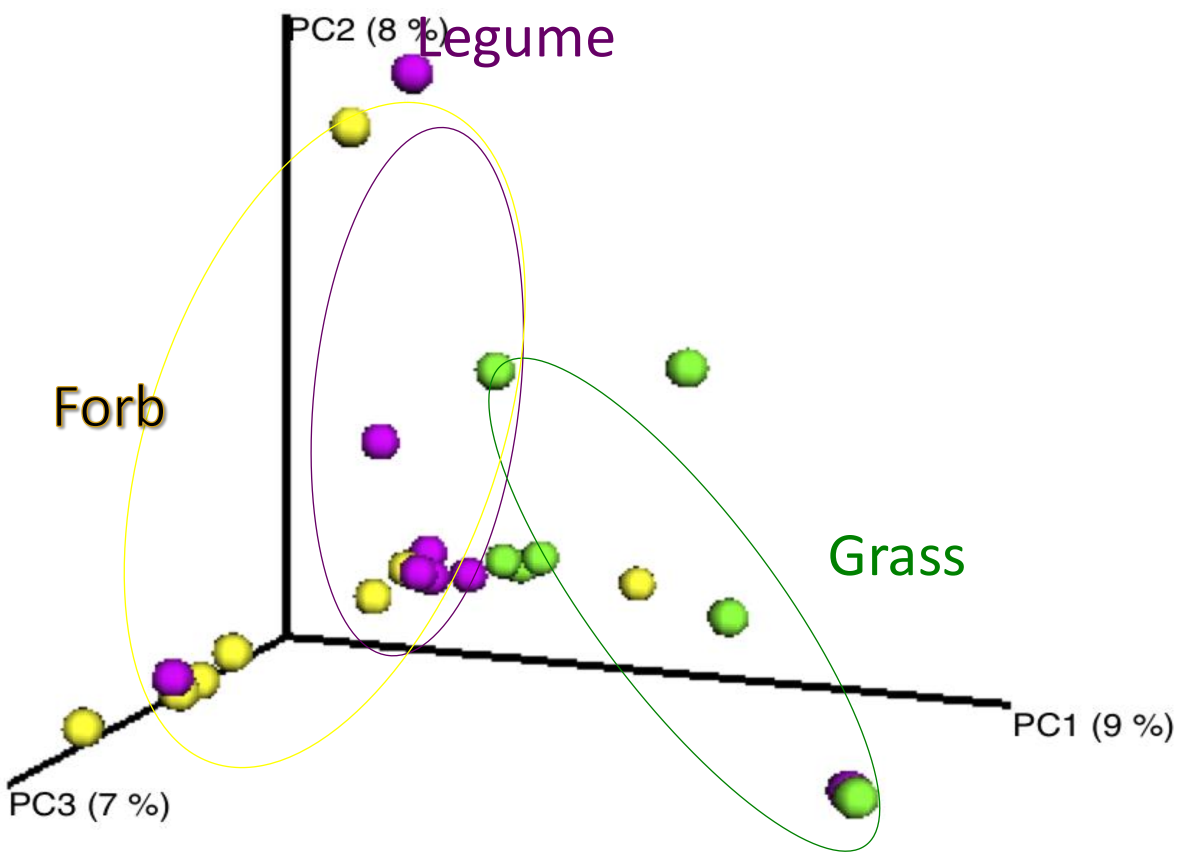
Ch4. Figure 9: Mass loss by litter type for collection 1 (November 2014).



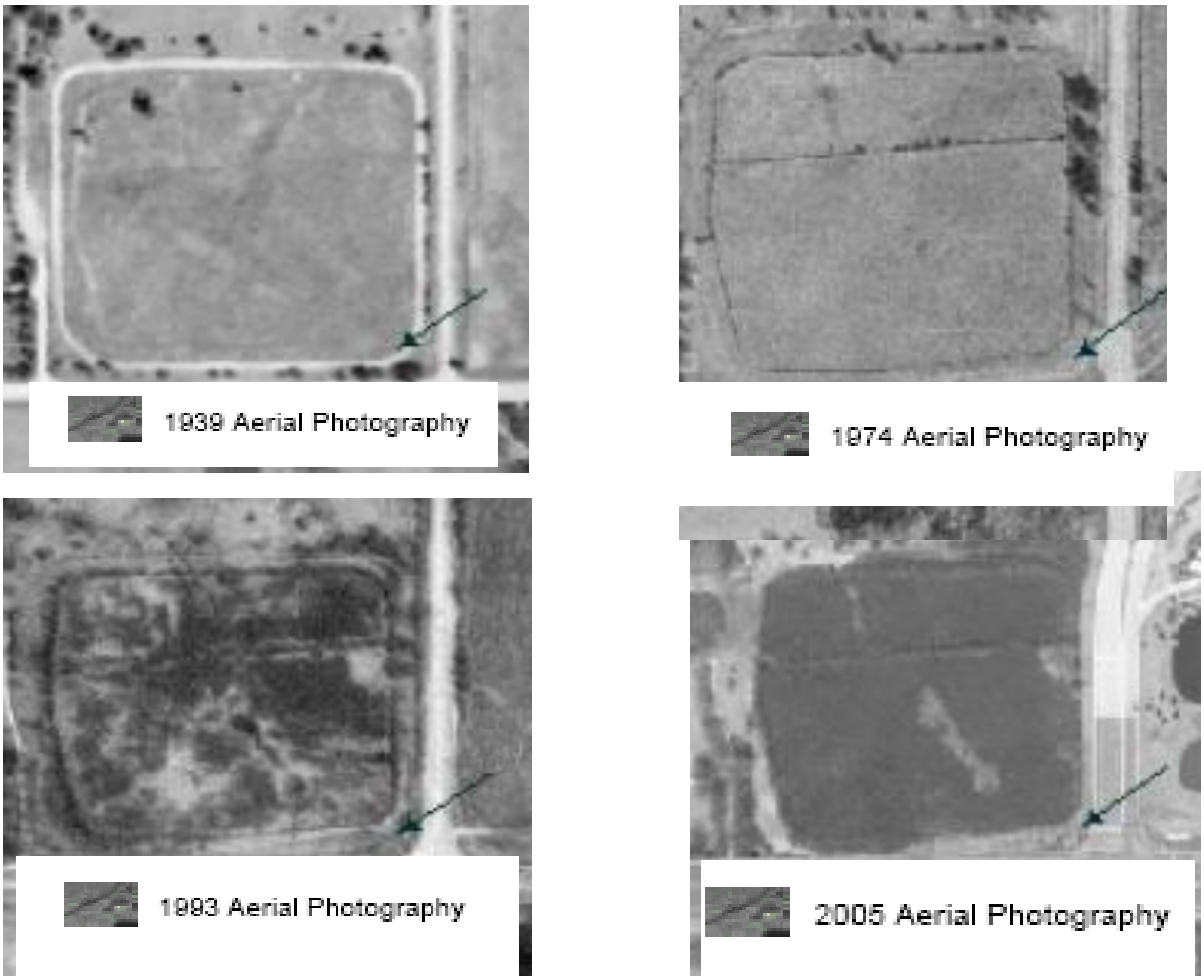
Ch4. Figure 10: Enzyme activity by leaf litter type.



Ch4. Figure 11: Fungal community composition by management use category.



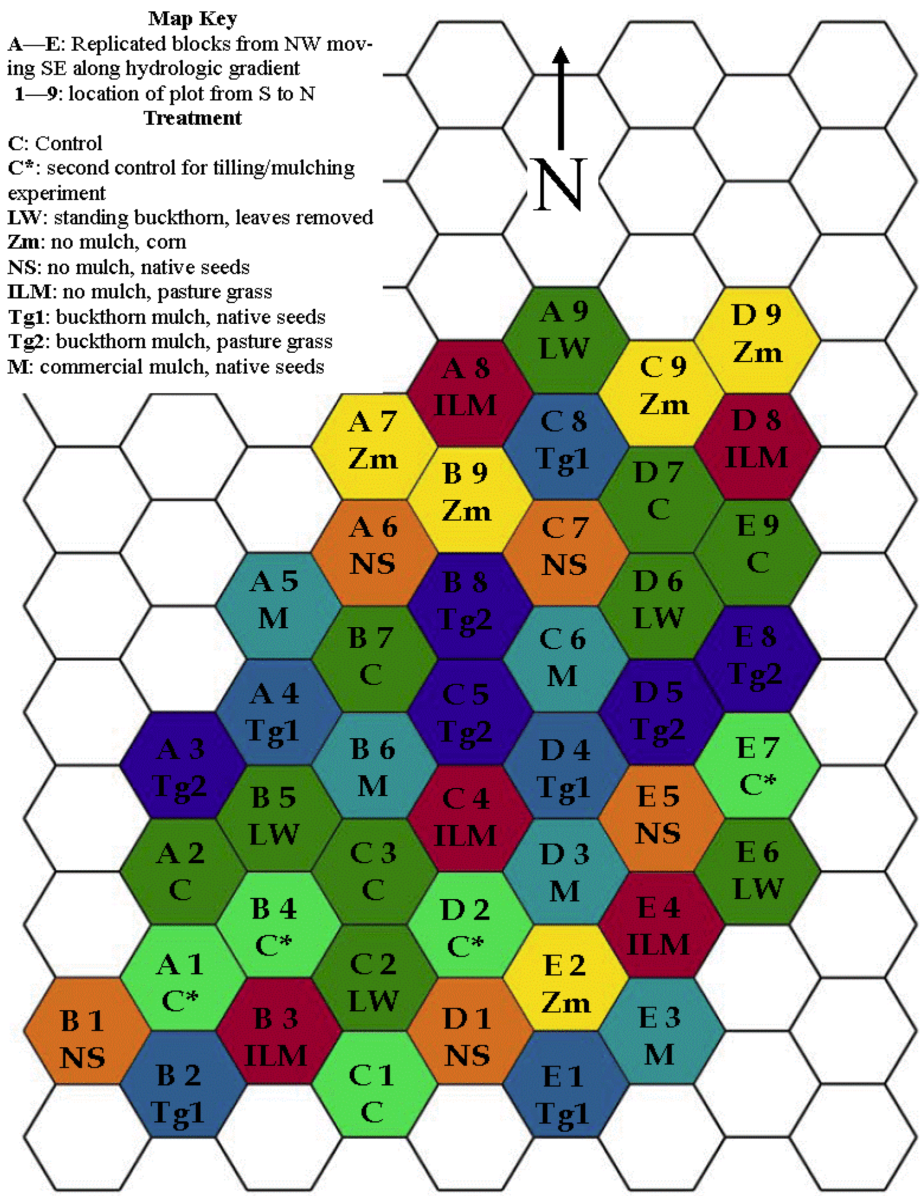
Ch4. Figure 12: Fungal community composition by leaf litter type.



Ch5. Figure 1: Historical aerial images of study site, showing progression from open field to buckthorn thicket.

Ch5. Table 1: Experimental Design.

Treatment	***Map Code***	***Soil Treatment***	***Plant Treatment***
Control	C	**none**	**None** standing buckthorn
No Mulch/ Native Seed	NS	**none**	**Native** seed mix applied in fall
No Mulch/ Cover Crop	ILM	**none**	**Pasture grass** seed mix applied in spring
No Mulch/ Corn crop	Zm	**none**	**Corn (feed)** grown and harvested
Commercial Mulch/ Native Seed	M	**Standard mulch** incorporated into the soil	**Native** seed mix applied in fall
Buckthorn Mulch/ Native Seed	Tg1	**Buckthorn mulch** incorporated into the soil	**Native** seed mix applied in fall
Buckthorn Mulch/ Cover Crop	Tg2	**Buckthorn mulch** incorporated into the soil	**Pasture grass** seed mix applied in spring
Leaf Removal	LW	**Leaf litter removed** from soil surface in fall	**None** standing buckthorn

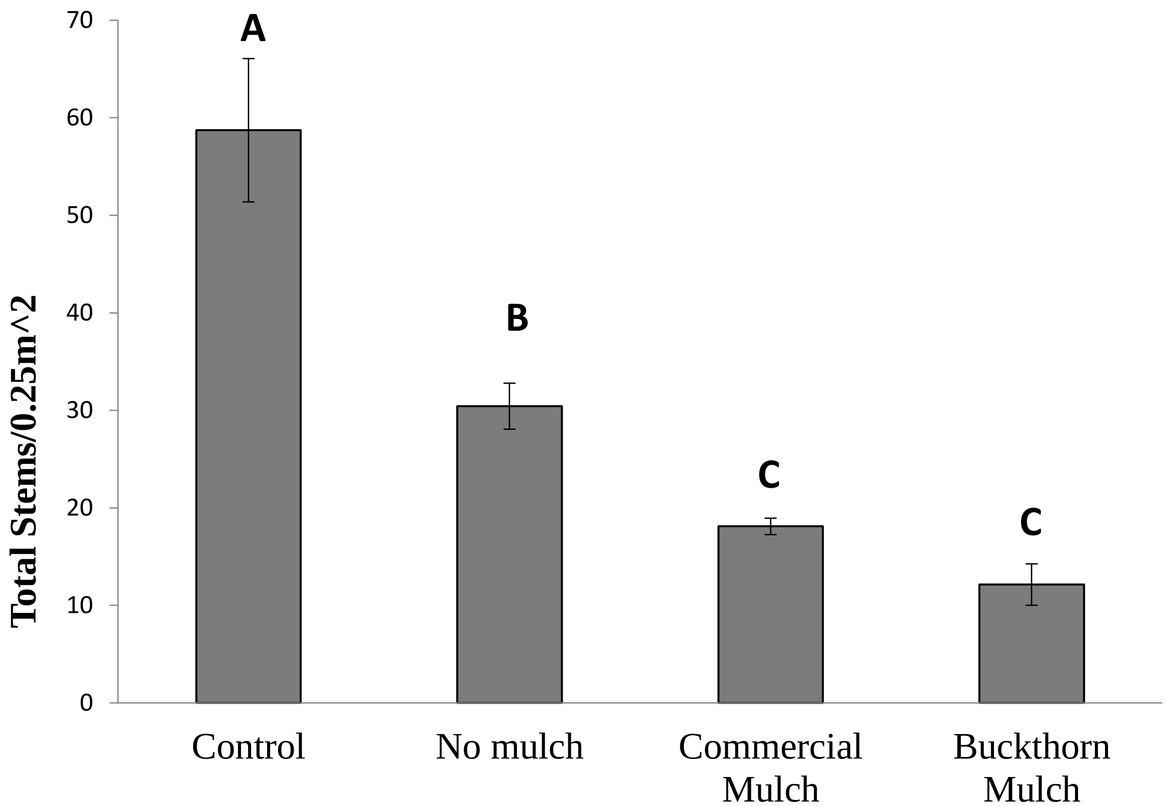


Ch5. Figure 2: Experimental design layout on 52m^2 hexagonal plots in randomized block design.

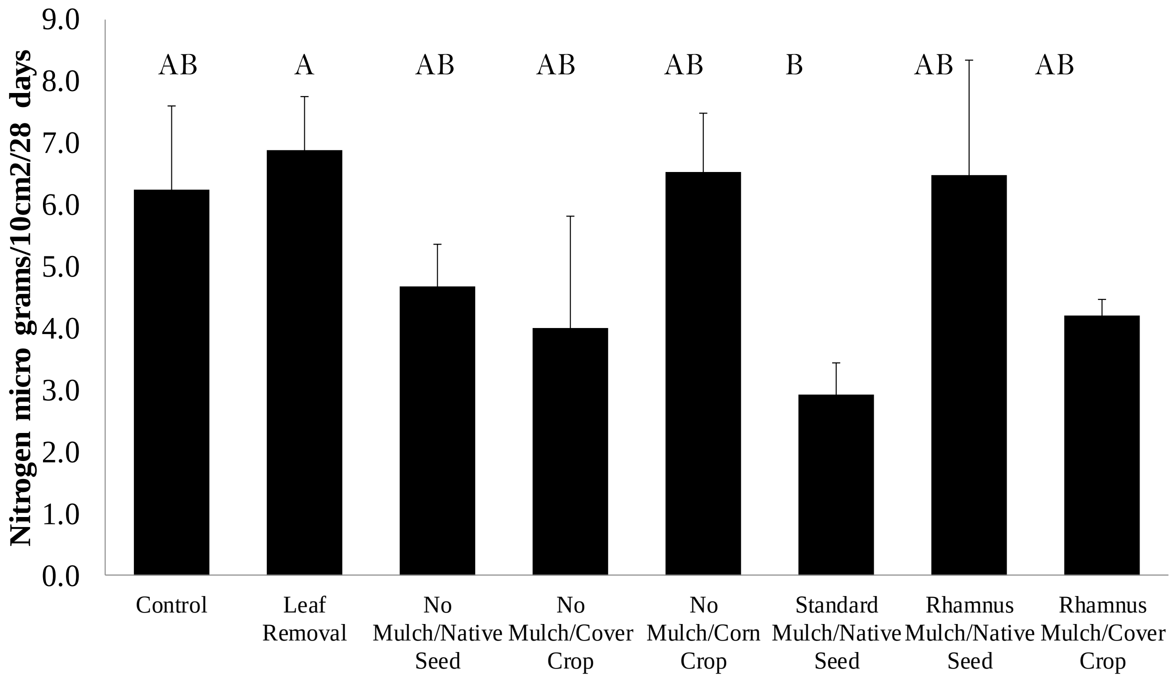
Ch5. Table 2: Greenhouse study experimental design.

Treatment	**Soil Type**	**Amendments**
No Mulch	3:2 - *R. cathartica* invaded soil: Sand	None
Commercial Mulch	3:2 - *R. cathartica* invaded soil: Sand	50 ml Chipped commercially available (Ecology's Best) mulch
Buckthorn Mulch	3:2 - *R. cathartica* invaded soil: Sand	50 ml Chipped Buckthorn mulch from Mettawa

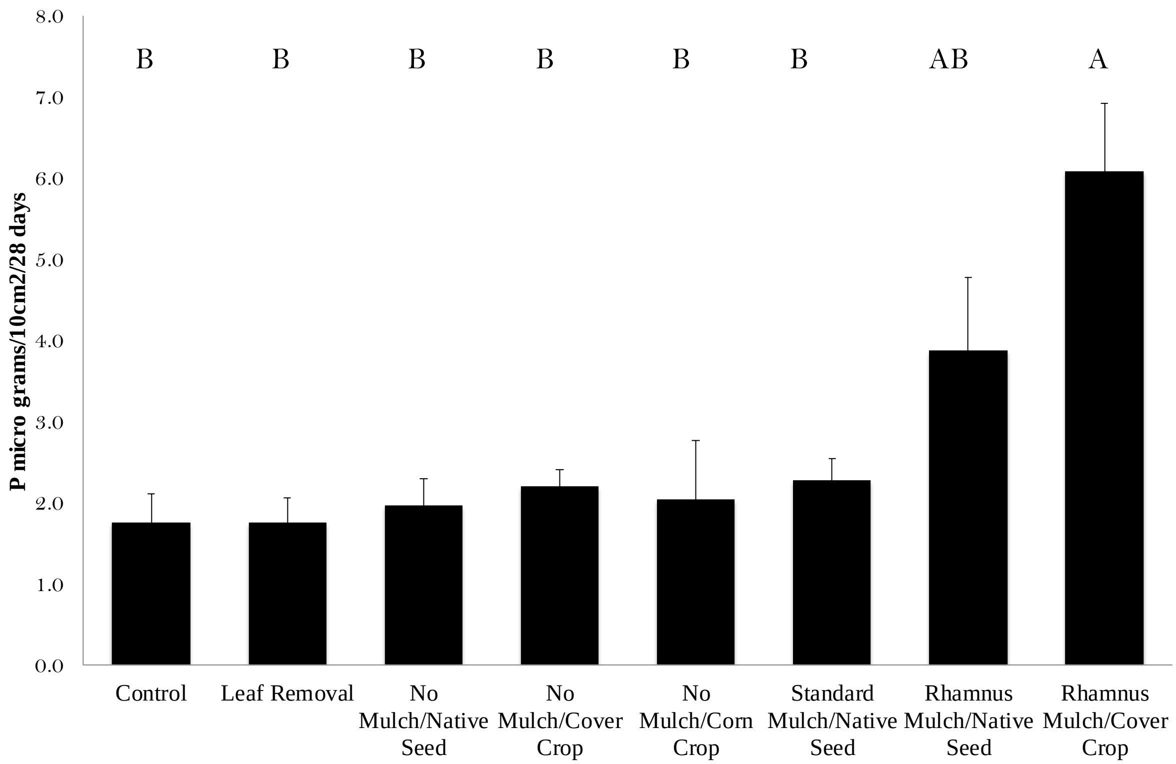
Ch5. Figure 3: Greenhouse study set-up showing randomized arrangement of field-collected buckthorn saplings.



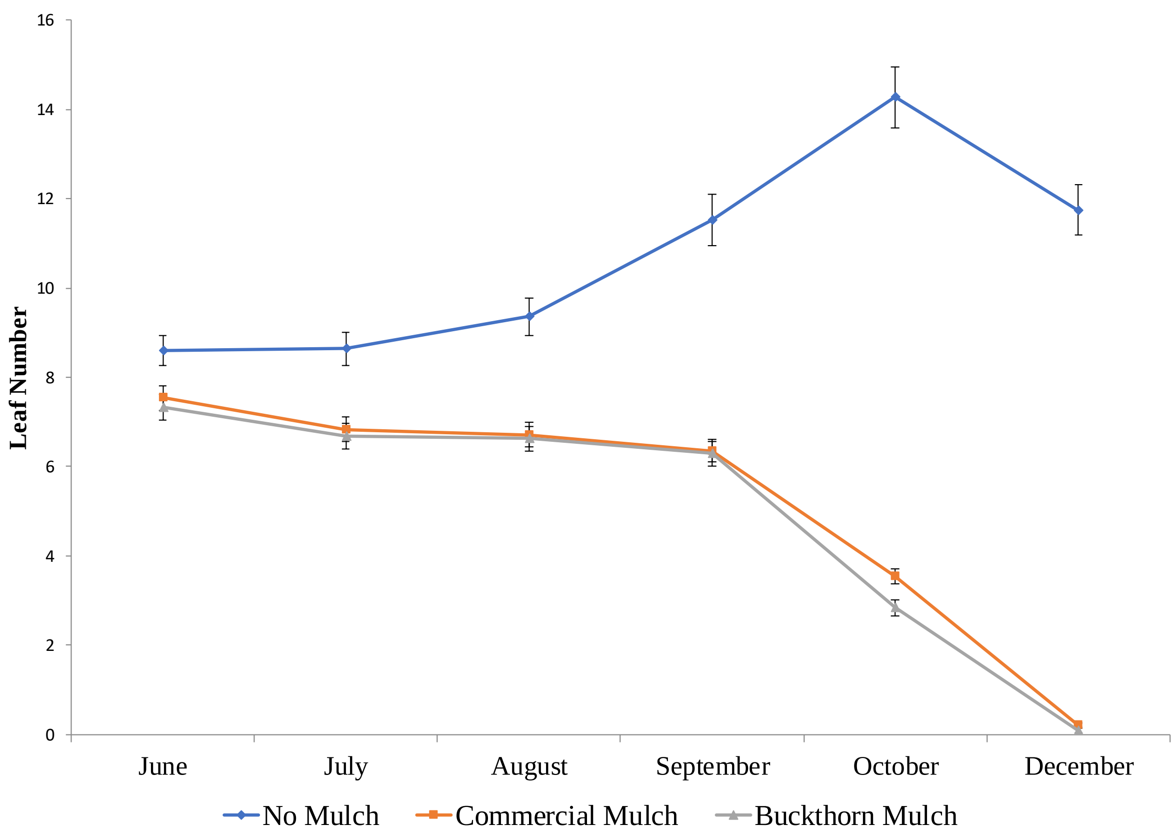
Ch5. Figure 4: Total buckthorn reinvasion (saplings and seedlings), mean per plot from 2008-2011. Different letters indicate significant differences in pair-wise comparisons.



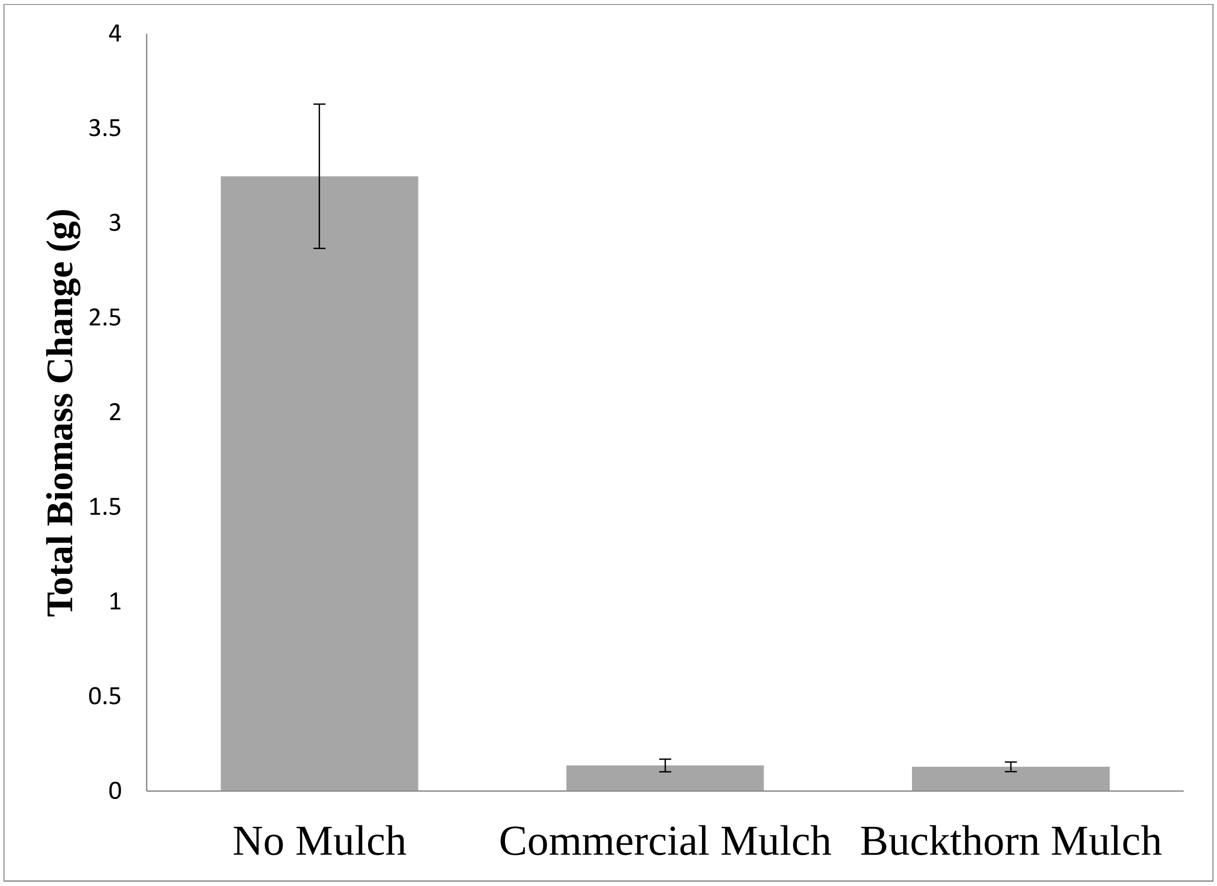
Ch5. Figure 5: Total inorganic nitrogen availability.



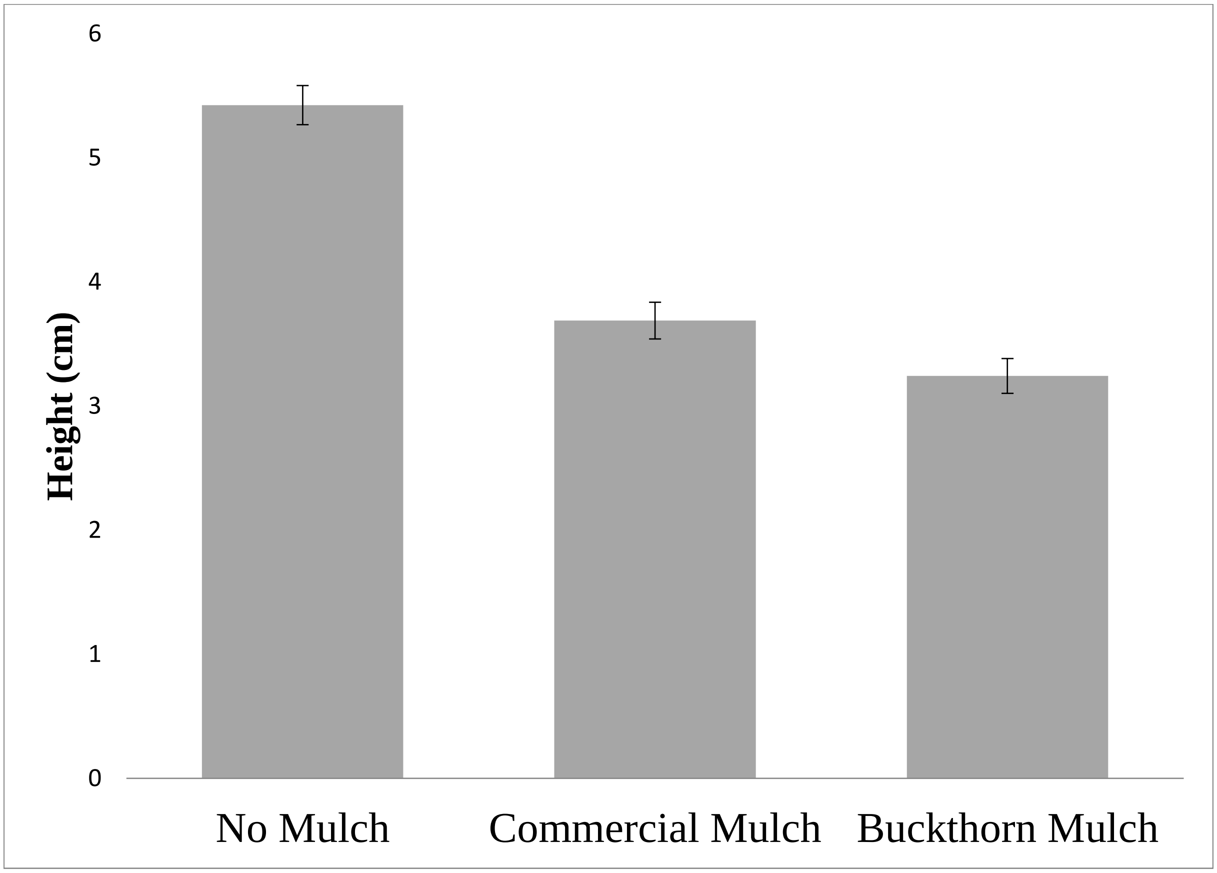
Ch5. Figure 6: Phosphorus availability by treatment.



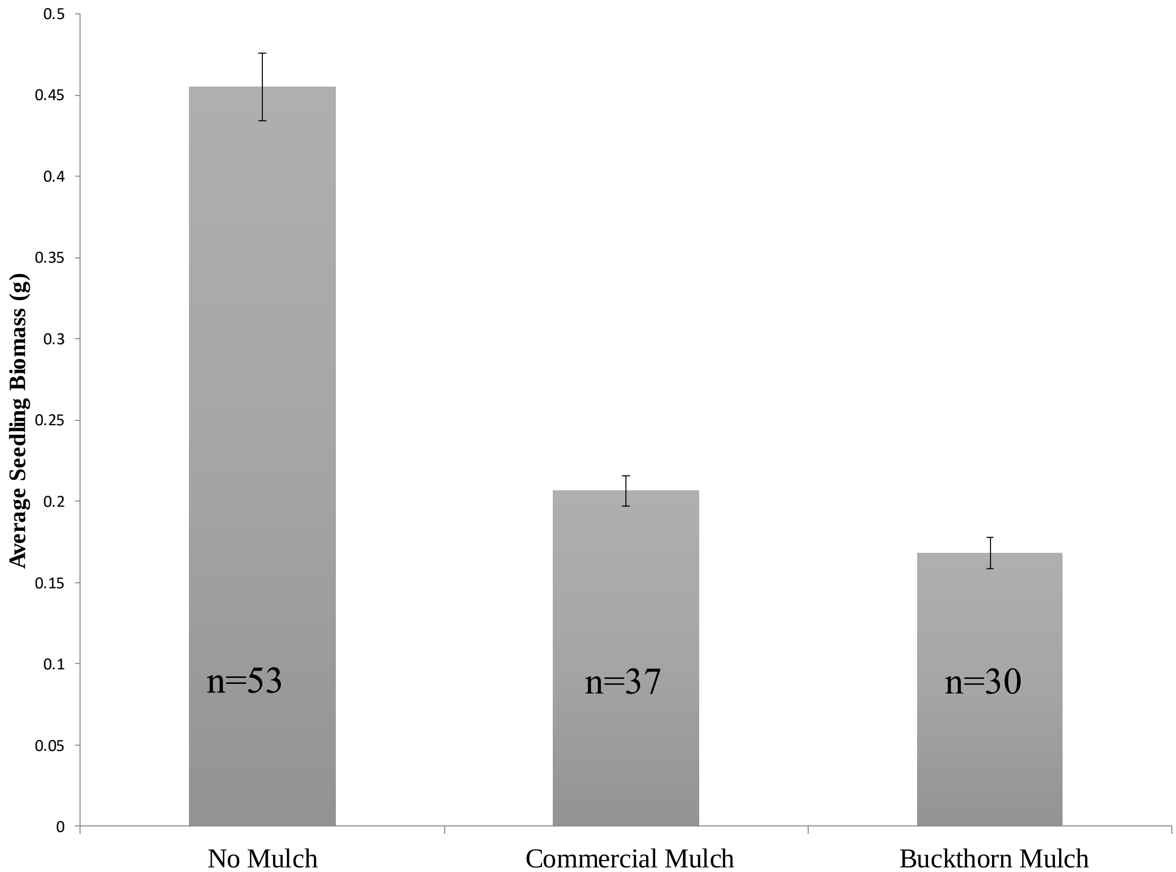
Ch4. Figure 7: Field collected sapling leaf number over time.



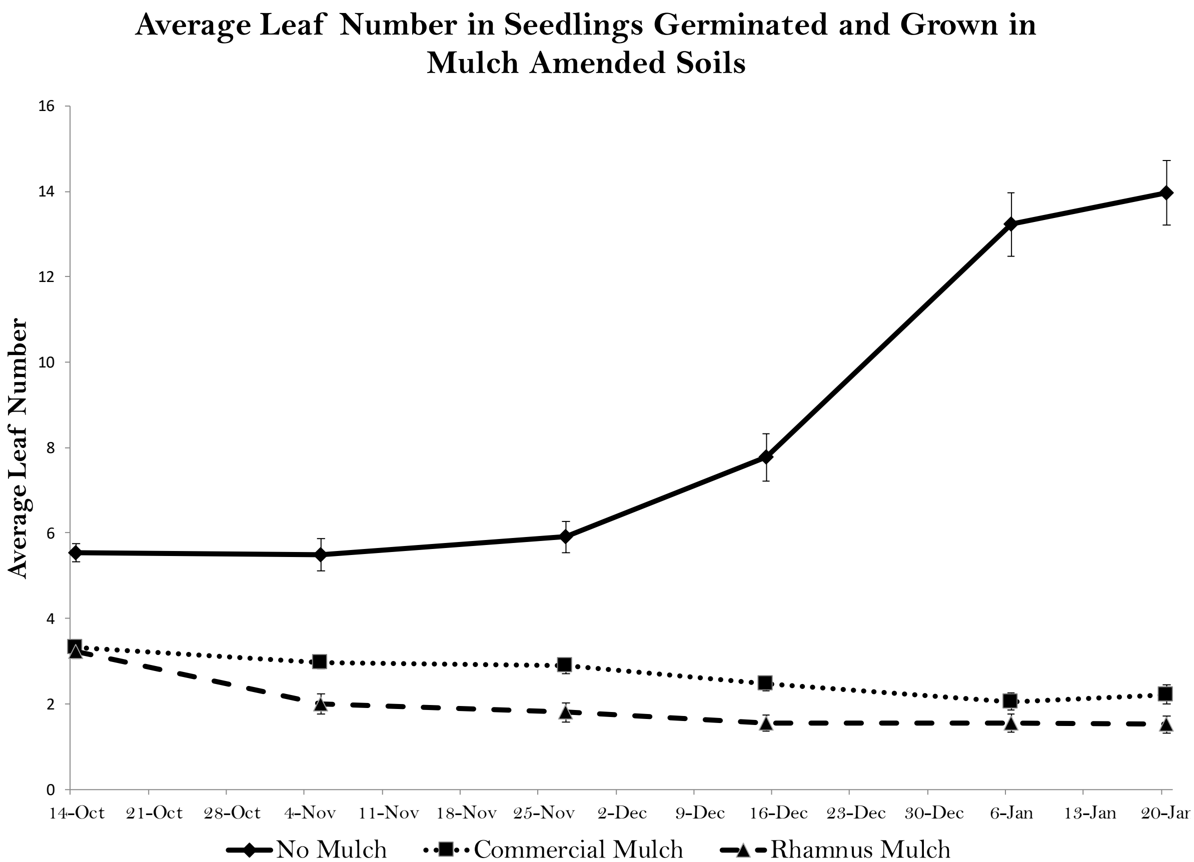
Ch5. Figure 8: Total biomass change of field-collected saplings 7 months.



Ch4. Figure 9: Mean height of field-collected saplings after 7 months.



Ch5. Figure 10: Number of seedlings germinated and mean biomass of germinated seedlings.



Ch5. Figure 11: Mean leaf number in seedlings germinated and grown in mulch amended soils.

Works Cited

Aerts, R., and H. de Caluwe. 1997. Nutritional and plant-mediated controls on leaf litter decomposition of *Carex* species. Ecology **78**:244-260.

Alguacil, M. d. M., Z. Lozano, M. J. Campoy, and A. Roldán. 2010. Phosphorus fertilisation management modifies the biodiversity of AM fungi in a tropical savanna forage system. Soil Biology and Biochemistry **42**:1114-1122.

Allen, E. B., W. W. Covington, and D. A. Falk. 1997. Developing the conceptual basis for restoration ecology. Restoration Ecology **5**:275-276.

Allison, S. D. 2005. Enzyme assays for fresh litter and soil.

Allison, S. D., and J. B. H. Martiny. 2008. Resistance, resilience, and redundancy in microbial communities. Proceedings of the National Academy of Sciences **105**:11512-11519.

Allison, S. D., and P. M. Vitousek. 2004. Extracellular Enzyme Activities and Carbon Chemistry as Drivers of Tropical Plant Litter Decomposition. BIOTROPICA **36**:285-296.

Andersson, E., T. McPhearson, P. Kremer, E. Gomez-Baggethun, D. Haase, M. Tuvendal, and D. Wurster. 2015. Scale and context dependence of ecosystem service providing units. Ecosystem Services **12**:157-164.

Asbjornsen, H., L. A. Brudvig, C. M. Mabry, C. W. Evans, and H. M. Karnitz. 2005. Defining reference information for restoring ecologically rare tallgrass oak savannas in the Midwestern United States. Journal Of Forestry **103**:345-350.

Ashworth, S. M., B. L. Foster, and K. Kindscherl. 2006. Relative contributions of adjacent species set and environmental conditions to plant community richness and composition in a group of created wetlands. Wetlands **26**:193-204.

Atkinson, I.-A.-E. 2001. Introduced mammals and models for restoration. Biological Conservation.

Atkinson, I. A. E. 1988. Presidential-Address - Opportunities For Ecological Restoration. New Zealand Journal Of Ecology **11**:1-12.

Averett, J. M., R. A. Klips, L. E. Nave, S. D. Frey, and P. S. Curtis. 2004. Effects of Soil Carbon Amendment on Nitrogen Availability and Plant Growth in an Experimental Tallgrass Prairie Restoration. Restoration Ecology **12**:568-574.

Baar, J. 1996. The ectomycorrhizal flora of primary and secondary stands of *Pinus sylvestris* in relation to soil conditions and ectomycorrhizal succession. Journal of Vegetation Science **7**:497-504.

Baar, J. a. N. L. S. 2000. Ectomycorrhizal fungi challenged by saprotrophic basidiomycetes and soil microfungi under different ammonium regimes in vitro. Mycologial Research **104**:691-697.

Baer, S., D. Kitchen, J. Blair, and C. Rice. 2002. Changes in ecosystem structure and function along a chronosequence of restored grasslands. Ecological Applications **12**:1688-1701.

Baer, S. G., J. M. Blair, S. L. Collins, and A. K. Knapp. 2004. Plant community responses to resource availability and heterogeneity during restoration. Oecologia **139**:617-629.

Baer, S. G., S. L. Collins, J. M. Blair, A. K. Knapp, and A. K. Fiedler. 2005. Soil heterogeneity effects on tallgrass prairie community heterogeneity: An application of ecological theory to restoration ecology. Restoration Ecology **13**:413-424.

Bauer, J. 2012. Invasive species: “back-seat drivers” of ecosystem change? Biological Invasions **14**:1295-1304.

Benayas, J. M. R., A. C. Newton, A. Diaz, and J. M. Bullock. 2009. Enhancement of Biodiversity and Ecosystem Services by Ecological Restoration: A Meta-Analysis. Science **325**:1121-1124.

Berg, B., and E. Matzner. 1997. Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. Environmental Reviews **5**:1-25.

Bleier, J. S., and R. D. Jackson. 2007. Manipulating the Quantity, Quality, and Manner of C Addition to Reduce Soil Inorganic N and Increase C4:C3 Grass Biomass. Restoration Ecology **15**:688-695.

Blumenthal, D. M. 2005. Interrelated Causes of Plant Invasion. Science **310**.

Blumenthal, D. M., N. R. Jordan, and M. Russelle. 2003a. Soil Carbon Addition Controls Weeds and Facilitates Prairie Restoration. Ecological Applications **13**:605-615.

Blumenthal, D. M., N. R. Jordan, and M. P. Russelle. 2003b. Soil carbon addition controls weeds and facilitates prairie restoration. Ecological Applications **13**:605-615.

Boerner, R. E. J., B. G. DeMars, and P. N. Leicht. 1996. Spatial patterns of mycorrhizal infectiveness of soils long a successional chronosequence. Mycorrhiza **6**:79-90.

Bohlen, P. J., S. Scheu, C. M. Hale, M. A. McLean, S. Migge, P. M. Groffman, and D. Parkinson. 2004. Non-native invasive earthworms as agents of change in northern temperate forests. Frontiers in Ecology and the Environment **2**:427-435.

Botkin, D. B., and C. E. Beveridge. 1997. Cities as environments. Urban Ecosystems **1**:3-19.

Brawn, J. D., and D. F. Stotz. 2001. The importance of the Chicago region and the “Chicago Wilderness” initiative for avian conservation. Pages 509-522 *in* J. M. Marzluff, R.

Bowman, and R. Donnelly, editors. Avian Ecology and Conservation in an Urbanizing World. Springer US, Boston, MA.

Callahan, J. T. 1984. Long-Term Ecological Research. BioScience **34**:363-367.

Caporaso, J. G., J. Kuczynski, J. Stombaugh, K. Bittinger, F. D. Bushman, E. K. Costello, N. Fierer, A. G. Pena, J. K. Goodrich, and J. I. Gordon. 2010. QIIME allows analysis of high-throughput community sequencing data. Nature methods **7**:335-336.

Carnovale, D. 2013. Enzyme Activity Assay Protocol.

Ceulemans, T., C. J. Stevens, L. Duchateau, H. Jacquemyn, D. J. G. Gowing, R. Merckx, H. Wallace, N. van Rooijen, T. Goethem, R. Bobbink, E. Dorland, C. Gaudnik, D. Alard, E. Corcket, S. Muller, N. B. Dise, C. Dupré, M. Diekmann, and O. Honnay. 2014. Soil phosphorus constrains biodiversity across European grasslands. Global Change Biology **20**:3814-3822.

Chapin, F. S., B. H. Walker, R. J. Hobbs, D. U. Hooper, J. H. Lawton, O. E. Sala, and D. Tilman. 1997. Biotic Control over the Functioning of Ecosystems. Science **277**:500-504.

Chengzhang, L., P. Ronghao, L. Yiqi, Z. Xuhui, W. Xiaowen, F. Changming, C. Jiakuan, and L. Bo. 2008. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. New Phytologist **177**:706-714.

Cherwin, K. L., T. R. Seastedt, and K. N. Suding. 2009. Effects of Nutrient Manipulations and Grass Removal on Cover, Species Composition, and Invasibility of a Novel Grassland in Colorado. Restoration Ecology **17**:818-826.

Choi, Y. D. 2004. Theories for ecological restoration in changing environment: Toward ‘futuristic’ restoration. Ecological Research **19**:75-81.

Claridge, A. W., S. C. Barry, S. J. Cork, and J. M. Trappe. 2000. Diversity and habitat relationships of hypogeous fungi: Factors influencing the occurrence and number of taxa. Biodiversity and Conservation **9**:175-199.

Clegg, C. D., R. D. L. Lovell, and P. J. Hobbs. 2003. The impact of grassland management regime on the community structure of selected bacterial groups in soils. FEMS Microbiology Ecology **43**:263-270.

Conn, C., and J. Dighton. 2000. Litter quality influences on decomposition, ectomycorrhizal community structure and mycorrhizal root surface acid phosphatase activity. Soil Biology & Biochemistry **32**:489-496.

Conway, D. R., J.C. Frankland, V.A. Saunders, and D.R. Wilson,. 2000. Effects ofelevated atmospheric CO2 on fungal competition and decomposition of *Fraxinus excelsior* litter in laboratory microcosms. Mycologial Research **104**:187-197.

Corbin, J. D., and C. M. D'Antonio. 2004. Can Carbon Addition Increase Competitiveness of Native Grasses? A Case Study from California. Restoration Ecology **4**:36-43.

Cortina, J., F. T. Maestre, R. Vallejo, M. J. Baeza, A. Valdecantos, and M. Pérez-Devesa. 2006. Ecosystem structure, function, and restoration success: Are they related? Journal for Nature Conservation **14**:152-160.

Council, C. R. B. 1999. Biodiversity recovery plan. Chicago, IL.

Cui, Q. G., and W. M. He. 2009. Soil biota, but not soil nutrients, facilitate the invasion of Bidens pilosa relative to a native species Saussurea deltoidea. Weed Research **49**:201-206.

Daehler, C. C. 2003. Performance Comparisons of Co-Occurring Native and Alien Invasive Plants: Implications for Conservation and Restoration. Annual Review of Ecology, Evolution, and Systematics **34**:183-211.

Dale, V. H., and S. C. Beyeler. 2001. Challenges in the development and use of ecological indicators. Ecological Indicators **1**:3-10.

Dassonville, N., S. Vanderhoeven, V. Vanparys, M. Hayez, W. Gruber, and P. Meerts. 2008. Impacts of alien invasive plants on soil nutrients are correlated with initial site conditions in NW Europe. Oecologia **157**:131-140.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology **88**:528-534.

Díaz, S., and M. Cabido. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution **16**:646-655.

Drake, J. A. 1990. The mechanics of community assembly and succession. Journal of Theoretical Biology **147**:213-233.

Durall, D. M., A.W. Todd, and J.M. Trappe, . 1994. Decomposition of C-14-labeled substrates by ectomycorrhizal fungi in association with Douglas fir. New Phytologist **127**:725-729.

Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems **6**:503-523.

Ehrenfeld, J. G., and N. Scott. 2001. Invasive species and the soil: effects on organisms and ecosystem processes. Ecological Applications **11**:1259-1260.

Eisenhauer, N., J. Schlaghamerský, P. B. Reich, and L. E. Frelich. 2011. The wave towards a new steady state: effects of earthworm invasion on soil microbial functions. Biological Invasions **13**:2191-2196.

Elgersma, K. J., J. G. Ehrenfeld, S. Yu, and T. Vor. 2011. Legacy effects overwhelm the short-term effects of exotic plant invasion and restoration on soil microbial community structure, enzyme activities, and nitrogen cycling. Oecologia **167**:733-745.

Elliott, E. 1986. Aggregate structure and carbon, nitrogen, and phosphorus in native and cultivated soils. Soil Science Society of America Journal **50**:627-633.

Fang, Y., F. Xun, W. Bai, W. Zhang, and L. Li. 2012. Long-Term Nitrogen Addition Leads to Loss of Species Richness Due to Litter Accumulation and Soil Acidification in a Temperate Steppe. PLoS ONE **7**:e47369.

Ferris, R., A. J. Peace, and A. C. Newton. 2000. Macrofungal communities of lowland Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karsten.) plantations in England: relationships with site factors and stand structure. Forest Ecology and Management **131**:255-267.

Ferry, B. W. a. N. D. 1968. Carbon nutrition of some mycorrhizal Boletus species. Transactions of the British Mycology Society, **51**:795-798.

Fierer, N., J. Ladau, J. C. Clemente, J. W. Leff, S. M. Owens, K. S. Pollard, R. Knight, J. A. Gilbert, and R. L. McCulley. 2013. Reconstructing the Microbial Diversity and Function of Pre-Agricultural Tallgrass Prairie Soils in the United States. Science **342**:621-624.

Fonseca, C. R., and G. Ganade. 2001. Species functional redundancy, random extinctions and the stability of ecosystems. Journal of Ecology **89**:118-125.

Frankland, J. C. 1998. Fungal succession: unraveling the unpredictable. Mycologial Research **102**:1-15.

Fraser, R. H., I. Olthof, and D. Pouliot. 2009. Monitoring land cover change and ecological integrity in Canada's national parks. Remote Sensing of Environment **113**:1397-1409.

Gambolati, G., and G. Volpi. 1979. A conceptual deterministic analysis of the kriging technique in hydrology. Water Resources Research **15**:625-629.

Gazol, A., and R. Ibáñez. 2009. Different response to environmental factors and spatial variables of two attributes (cover and diversity) of the understorey layers. Forest Ecology and Management **258**:1267-1274.

German, D. P., M. N. Weintraub, A. S. Grandy, C. L. Lauber, Z. L. Rinkes, and S. D. Allison. 2011. Optimization of hydrolytic and oxidative enzyme methods for ecosystem studies. Soil Biology and Biochemistry **43**:1387-1397.

Gobster, P. H. 1997. The Chicago wilderness and its critics: the other side: a survey of arguments.

Gramss, G., D. Ziegenhagen, and S. Sorge, . 1999. Degradation of soil humic extract by wood- and soil-associated fungi, bacteria, and commercial enzymes. Microbial Ecology **37**:140-151.

Grimm, N. B., S. H. Faeth, N. E. Golubiewski, C. L. Redman, J. Wu, X. Bai, and J. M. Briggs. 2008. Global Change and the Ecology of Cities. Science **319**:756-760.

Groffman, P. M., M. L. Cadenasso, J. Cavender-Bares, D. L. Childers, N. B. Grimm, J. M. Grove, S. E. Hobbie, L. R. Hutyra, G. Darrel Jenerette, T. McPhearson, D. E. Pataki, S.

T. A. Pickett, R. V. Pouyat, E. Rosi-Marshall, and B. L. Ruddell. 2017. Moving Towards a New Urban Systems Science. Ecosystems **20**:38-43.

Gunn, A. 1992. The use of mustard to estimate earthworm populations. Pedobiologia **36**:65-67.

Hale, C. M., L. E. Frelich, and P. B. Reich. 2005. Exotic European earthworm invasion dynamics in northern hardwood forests of Minnesota, USA. Ecological Applications **15**:848-860.

Hansen, M. J., and D. J. Gibson. 2014. Use of multiple criteria in an ecological assessment of a prairie restoration chronosequence. Applied Vegetation Science **17**:63-73.

Harris, J. A. 2003. Measurements of the soil microbial community for estimating the success of restoration. European Journal of Soil Science **54**:801-808.

Helford, R. M. 2000. Constructing nature as constructing science: Expertise, activist science, and public conflict in the Chicago Wilderness.

Heneghan, L., F. Fatemi, L. Umek, K. Grady, K. Fagen, and M. Workman. 2006. The invasive shrub European buckthorn (Rhamnus cathartica, L.) alters soil properties in Midwestern U.S. woodlands. Applied Soil Ecology **32**:142-148.

Heneghan, L., S. P. Miller, S. Baer, M. A. Callaham Jr, J. Montgomery, M. Pavao-Zuckerman, C. C. Rhoades, and S. Richardson. 2008a. Integrating Soil Ecological Knowledge into Restoration Management. Restoration Ecology **16**:608-617.

Heneghan, L., C. Mulvaney, K. Ross, L. Umek, C. Watkins, L. M. Westphal, and D. H. Wise. 2012. Lessons Learned from Chicago Wilderness—Implementing and Sustaining Conservation Management in an Urban Setting. Diversity **4**:74-93.

Heneghan, L., C. Mulvaney, and L. Umek. 2007a. Developing A Scientific Research Agenda for Chicago Wilderness.

Heneghan, L., J. Steffen, and K. Fagen. 2007b. Interactions of an introduced shrub and introduced earthworms in an Illinois urban woodland: impact on leaf litter decomposition. Pedobiologia **50**:543-551.

Heneghan, L., L. Umek, B. Bernau, K. Grady, J. Iatropulos, D. Jabon, and M. Workman. 2008b. Ecological research can augment restoration practice in urban areas degraded by invasive species—examples from Chicago Wilderness. Urban Ecosystems **12**:63-77.

Heneghan, L., L. Umek, B. Bernau, K. Grady, J. Iatropulos, D. Jabon, and M. Workman. 2009. Ecological research can augment restoration practice in urban areas degraded by invasive species—examples from Chicago Wilderness. Urban Ecosystems **12**:63-77.

Hobbs, R. J. 2007. Setting Effective and Realistic Restoration Goals: Key Directions for Research. Restoration Ecology **15**:354-357.

Hobbs, R. J., A. Jentsch, and V. M. Temperton. 2007. Restoration as a Process of Assembly and Succession Mediated by Disturbance. Pages 150-167 *in* L. R. Walker, J. Walker, and R. J. Hobbs, editors. Linking Restoration and Ecological Succession. Springer New York, New York, NY.

Holmer, L., P. Renvall, and J. Stenlid. 1997. Selective replacement between species of wood-rotting basidiomycetes, a laboratory study. Mycologial Research **101**:714-720.

Holmer, L., and J. Stenlid. 1996. Diffuse competition for heterogeneous substrate in soil among six species of wood-decomposing basidiomycetes. . Oecologia **106**:531-538.

Iannone, B. V., S. M. Galatowitsch, and C. J. Rosen. 2008. Evaluation of resource-limiting strategies intended to prevent Phalaris arundinacea (reed canarygrass) invasions in restored sedge meadows. Ecoscience **15**:508-518.

Iannone, B. V., L. Heneghan, D. Rijal, and D. H. Wise. 2015. Below-ground causes and consequences of woodland shrub invasions: a novel paired-point framework reveals new insights. Journal of Applied Ecology **52**:78-88.

Iannone III, B. V., and S. M. Galatowitsch. 2008. Altering Light and Soil N to Limit Phalaris arundinacea Reinvasion in Sedge Meadow Restorations. Restoration Ecology **16**:689-701.

Iannone III, B. V., S. M. Galatowitsch, and C. J. Rosen. 2008. Evaluation of resource-limiting strategies intended to prevent *Phalaris arundinacea* (reed canarygrass) invasions in restored sedge meadows. Ecoscience **15**:508-518.

Iannone III, B. V., C. J. Rosen, and S. M. Galatowitsch. 2009. Soil nitrogen concentrations in a restored sedge meadow wetland as affected by the application of high C:N amendments. Ecological Restoration **27**:193-199.

Iannone III, B. V., L. G. Umek, D. H. Wise, and L. Heneghan. 2012. A Simple, Safe, and Effective Sampling Technique for Investigating Earthworm Communities in Woodland Soils: Implications for Citizen Science. Natural Areas Journal **32**:283-292.

Institute, N. R. R. 2011. Research Methods. Great Lakes Worm Watch.

Janssens, F., A. Peeters, J. R. B. Tallowin, J. P. Bakker, R. M. Bekker, F. Fillat, and M. J. M. Oomes. 1998. Relationship between soil chemical factors and grassland diversity. Plant and Soil **202**:69-78.

Jiménez, J.-J., T. Decaëns, and J.-P. Rossi. 2012. Soil environmental heterogeneity allows spatial co-occurrence of competitor earthworm species in a gallery forest of the Colombian 'Llanos'. Oikos **121**:915-926.

Johnson, D. W., F. A. Dijkstra, and W. Cheng. 2007. The effects of Glycine max and Helianthus annuus on nutrient availability in two soils. Soil Biology and Biochemistry **39**:2160-2163.

Jonsson, L., A. Dahlberg, M. C. Nilsson, O. Zackrisson, and O. Karen. 1999. Ectomycorrhizal fungal communities in late-successional Swedish boreal forests, and their composition following wildfire. Molecular Ecology **8**:205-215.

Jordan, N. R., D. L. Larson, and S. C. Huerd. 2008. Soil modification by invasive plants: effects on native and invasive species of mixed-grass prairies. Biological Invasions **10**:177-190.

Jordan, W. R. 1997. The tallgrass restoration handbook: for prairies, savannas, and woodlands. Island Press.

Kandziora, M., B. Burkhard, and F. Müller. 2013. Interactions of ecosystem properties, ecosystem integrity and ecosystem service indicators—A theoretical matrix exercise. Ecological Indicators **28**:54-78.

Kardol, P., N. J. Cornips, M. M. L. van Kempen, J. M. T. Bakx-Schotman, and W. H. van der Putten. 2007. Microbe-mediated plant-soil feedback causes historical contingency effects in plant community assembly. Ecological Monographs **77**:147-162.

Kaye, J. P., P. M. Groffman, N. B. Grimm, L. A. Baker, and R. V. Pouyat. 2006. A distinct urban biogeochemistry? Trends in Ecology & Evolution **21**:192-199.

Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. Nature **417**:636-638.

Kettenring, K. M., and C. R. Adams. 2011. Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. Journal of Applied Ecology **48**:970-979.

Klironomos, J. N., P. Widden, and I. Deslandes. 1992. Feeding preferences of the collembolan Folsomia candida in relation to microfungal successions on decaying litter. Soil Biology & Biochemistry **24**:685-692.

Knight, K., J. Kurylo, A. Endress, J. Stewart, and P. Reich. 2007. Ecology and ecosystem impacts of common buckthorn (Rhamnus cathartica): a review. Biological Invasions **9**:925-937.

Knorr, M., S. D. Frey, and P. S. Curtis. 2005. Nitrogen additions and litter decomposition: a meta-analysis. Ecology **86**:3252-3257.

Koide, R. T., L. Suomi, C.M. Stevens, and L. McCormick. 1998. Interactions between needles of *Pinus resinosa* and ectomycorrhizal fungi. New Phytologist **140**:539-547.

Kourtev, P., W. Huang, and J. Ehrenfeld. 1999. Differences in earthworm densities and nitrogen dynamics in soils under exotic and native plant species. Biological Invasions **1**:237-245.

Kranabetter, J. M., and T. Wylie. 1998. Ectomycorrhizal community structure across forest openings on naturally regenerated western hemlock seedlings. . Canadian Journal of Botany **76**:189-196.

Kulmatiski, A., and K. H. Beard. 2006. Activated Carbon as a Restoration Tool: Potential for Control of Invasive Plants in Abandoned Agricultural Fields. Restoration Ecology **14**:251-257.

Kulmatiski, A., K. H. Beard, and J. M. Stark. 2006. Soil history as a primary control on plant invasion in abandoned agricultural fields. Journal of Applied Ecology **43**:868-876.

Kumar, S., T. J. Stohlgren, and G. W. Chong. 2006. Spatial heterogeneity influences natuve and nonnative plant speices richness. Ecology **87**:3186-3199.

Last, F. T., P. A. Mason, K. Ingleby, and L. V. Fleming. 1984. Succession of fruitbodies of sheathing mycorrhizal fungi associated with *Betula pendula*. Forest Ecology and Management **9**:229-234.

Lawrence, A. P., and M. A. Bowers. 2002. A test of the 'hot'mustard extraction method of sampling earthworms. Soil Biology and Biochemistry **34**:549-552.

Lepczyk, C. A., M. F. J. Aronson, K. L. Evans, M. A. Goddard, S. B. Lerman, and J. S. MacIvor. 2017. Biodiversity in the City: Fundamental Questions for Understanding the Ecology of Urban Green Spaces for Biodiversity Conservation. BioScience **67**:799-807.

Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. Oikos:15-26.

Liao, C., R. Peng, Y. Luo, X. Zhou, X. Wu, C. Fang, J. Chen, and B. Li. 2008. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. New Phytologist **177**:706-714.

Lindenmayer, D., R. J. Hobbs, R. Montague-Drake, J. Alexandra, A. Bennett, M. Burgman, P. Cale, A. Calhoun, V. Cramer, P. Cullen, D. Driscoll, L. Fahrig, J. Fischer, J. Franklin, Y. Haila, M. Hunter, P. Gibbons, S. Lake, G. Luck, C. MacGregor, S. McIntyre, R. M. Nally, A. Manning, J. Miller, H. Mooney, R. Noss, H. Possingham, D. Saunders, F. Schmiegelow, M. Scott, D. Simberloff, T. Sisk, G. Tabor, B. Walker, J. Wiens, J.

Woinarski, and E. Zavaleta. 2008. A checklist for ecological management of landscapes for conservation. Ecology Letters **11**:78-91.

Lindenmayer, D. B., and G. E. Likens. 2009. Adaptive monitoring: a new paradigm for long-term research and monitoring. Trends in Ecology & Evolution **24**:482-486.

Loreau, M. 2004. Does functional redundancy exist? Oikos **104**:606-611.

Loreau, m., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, and D. U. Hector. 2001. Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. Science **294**:804-808.

Lovell, R. D., S. C. Jarvis, and R. D. Bardgett. 1995. Soil microbial biomass and activity in long-term grassland: Effects of management changes. Soil Biology and Biochemistry **27**:969-975.

Lovett, G. M., M. M. Traynor, R. V. Pouyat, M. M. Carreiro, W.-X. Zhu, and J. W. Baxter. 2000. Atmospheric Deposition to Oak Forests along an Urban−Rural Gradient. Environmental Science & Technology **34**:4294-4300.

Lyons, K. G., and M. W. Schwartz. 2001. Rare species loss alters ecosystem function – invasion resistance. Ecology Letters **4**:358-365.

MacDougall, A. S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology **86**:42-55.

Madritch, M. D., and R. L. Lindroth. 2009. Removal of invasive shrubs reduces exotic earthworm populations. Biological Invasions **11**:663-671.

Manning, A. D., J. Fischer, and D. B. Lindenmayer. 2006. Scattered trees are keystone structures–implications for conservation. Biological Conservation **132**:311-321.

Martin, L. M., K. A. Moloney, and B. J. Wilsey. 2005. An assessment of grassland restoration success using species diversity components. Journal of Applied Ecology **42**:327-336.

Massicotte, H. B., R. Molina, L.E. Tackaberry, J.E. Smith, and M.P. Amaranthus. 1999. Diversity and host specificity of ectomycorrhizal fungi retrieved from three adjacent forest sites by five host species. Canadian Journal of Botany **77**:1053-1076.

McCary, M. A., J.-C. Martínez, L. Umek, L. Heneghan, and D. H. Wise. 2015. Effects of woodland restoration and management on the community of surface-active arthropods in the metropolitan Chicago region. Biological Conservation **190**:154-166.

McDonnell, M. J., S. T. A. Pickett, P. Groffman, P. Bohlen, R. V. Pouyat, W. C. Zipperer, R. W. Parmelee, M. M. Carreiro, and K. Medley. 1997. Ecosystem processes along an urban-to-rural gradient. Urban Ecosystems **1**:21-36.

McGuire, K. L., E. Bent, J. Borneman, A. Majumder, S. D. Allison, and K. K. Treseder. 2010. Functional diversity in resource use by fungi. Ecology **91**:2324-2332.

McGuire, K. L., and K. K. Treseder. 2010. Microbial communities and their relevance for ecosystem models: Decomposition as a case study. Soil Biology and Biochemistry **42**:529-535.

McKinney, M. 2008. Effects of urbanization on species richness: A review of plants and animals. Urban Ecosystems **11**:161-176.

Meier, C. L., and W. D. Bowman. 2008. Links between plant litter chemistry, species diversity, and below-ground ecosystem function. Proceedings of the National Academy of Sciences **105**:19780-19785.

Michener, W. K. 1997. Quantitatively Evaluating Restoration Experiments: Research Design, Statistical Analysis, and Data Management Considerations. Restoration Ecology **5**:324-337.

Michez, A., H. Piégay, F. Toromanoff, D. Brogna, S. Bonnet, P. Lejeune, and H. Claessens. 2013. LiDAR derived ecological integrity indicators for riparian zones: Application to the Houille river in Southern Belgium/Northern France. Ecological Indicators **34**:627-640.

Milcu, A., S. Partsch, C. Scherber, W. W. Weisser, and S. Scheu. 2008. Earthworms and legumes control litter decomposition in a plnat diversity gradient. Ecology **89**:1872-1882.

Miller, J. R., and R. J. Hobbs. 2007. Habitat Restoration—Do We Know What We're Doing? Restoration Ecology **15**:382-390.

Mitchell, C. P., and C. S. Millar. 1978. Mycofloral successions on Corsican pine needles colonized on trees by three different fungi. Transactions of the British Mycology Society, **71**:303-317.

Moore, M. M., C. A. Casey, J. D. Bakker, J. D. Springer, P. Z. Fule, W. W. Covington, and D. C. Laughlin. 2006. Herbaceous vegetation responses (1992–2004) to restoration treatments in a ponderosa pine forest. Rangeland Ecology & Management **59**:135-144.

Moorhead, D. L., and R. L. Sinsabaugh. 2006. A theoretical model of litter decay and microbial interaction. Ecological Monographs **76**:151-174.

Morghan, K. J. R., and T. R. Seastedt. 1999. Effects of Soil Nitrogen Reduction on Nonnative Plants in Restored Grasslands. Restoration Ecology **7**:51-55.

Mouillot, D., D. R. Bellwood, C. Baraloto, J. Chave, R. Galzin, M. Harmelin-Vivien, M. Kulbicki, S. Lavergne, S. Lavorel, N. Mouquet, C. E. T. Paine, J. Renaud, and W. Thuiller. 2013. Rare Species Support Vulnerable Functions in High-Diversity Ecosystems. PLOS Biology **11**:e1001569.

Nacke, H., A. Thürmer, A. Wollherr, C. Will, L. Hodac, N. Herold, I. Schöning, M. Schrumpf, and R. Daniel. 2011. Pyrosequencing-Based Assessment of Bacterial Community Structure Along Different Management Types in German Forest and Grassland Soils. PLoS ONE **6**:e17000.

Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos **91**:97-108.

Niemelä, J. 2014. Ecology of urban green spaces: The way forward in answering major research questions. Landscape and Urban Planning **125**:298-303.

Nikula, S., E. Vapaavuori, and S. Manninen. 2010. Urbanization-related changes in European aspen (Populus tremula L.): Leaf traits and litter decomposition. Environmental Pollution **158**:2132-2142.

Nilsson, M. C., D.A. Wardle, and A. Dahlberg, . 1999. Effects of plant litter species composition and diversity on the boreal forest plant-soil system. Oikos **86**:16-26.

Noss, R. F. 2000. High-risk ecosystems as foci for considering biodiversity and ecological integrity in ecological risk assessments. Environmental Science & Policy **3**:321-332.

Nuzzo, V. A., J. C. Maerz, and B. Blossey. 2009. Earthworm invasion as the driving force behind plant invasion and community change in northeastern North American forests. Conservation Biology **23**:966-974.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2015. vegan: Community Ecology Package. R package version 2.3-2.

Palmer, M. A., H. L. Menninger, and E. Bernhardt. 2010. River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? Freshwater biology **55**:205-222.

Pasqualetti, M., B. Mulas, L. Zucconi, and A. Rambelli. 1999. Succession of microfungal communities on *Myrtus communis* leaf litter in a Sardinian Mediterranean maquis ecosystem. Mycologial Research **103**:724-728.

Patra, A. K., L. Abbadie, A. Clays-Josserand, V. Degrange, S. J. Grayston, N. Guillaumaud, P. Loiseau, F. Louault, S. Mahmood, S. Nazaret, L. Philippot, F. Poly, J. I. Prosser, and X. L. Roux. 2006. Effects of management regime and plant species on the enzyme activity and genetic structure of N-fixing, denitrifying and nitrifying bacterial communities in grassland soils. Environmental Microbiology **8**:1005-1016.

Pavao-Zuckerman, M. A., and D. C. Coleman. 2005. Decomposition of chestnut oak (Quercus prinus) leaves and nitrogen mineralization in an urban environment. Biology and Fertility of Soils **41**:343-349.

Pavao-Zuckerman, M. A., and D. C. Coleman. 2007. Urbanization alters the functional composition, but not taxonomic diversity, of the soil nematode community. Applied Soil Ecology **35**:329-339.

Perring, M. P., R. J. Standish, J. N. Price, M. D. Craig, T. E. Erickson, K. X. Ruthrof, A. S. Whiteley, L. E. Valentine, and R. J. Hobbs. 2015. Advances in restoration ecology: rising to the challenges of the coming decades. Ecosphere **6**:1-25.

Perry, L. G., D. M. Blumenthal, T. A. Monaco, M. W. Paschke, and E. F. Redente. 2010. Immobilizing nitrogen to control plant invasion. Oecologia **163**:13-24.

Perry, L. G., S. M. Galatowitsch, and C. J. Rosen. 2004. Competitive control of invasive vegetation: a native wetland sedge suppresses Phalaris arundinacea in carbon-enriched soil. Journal of Applied Ecology **41**:151-162.

Phoenix, G. K., W. K. Hicks, S. Cinderby, J. C. I. Kuylenstierna, W. D. Stock, F. J. Dentener, K. E. Giller, A. T. Austin, R. D. B. Lefroy, B. S. Gimeno, M. R. Ashmore, and P. Ineson. 2006. Atmospheric nitrogen deposition in world biodiversity hotspots: the need for a greater global perspective in assessing N deposition impacts. Global Change Biology **12**:470-476.

Pieri, D. S., L. G. Umek, and L. Heneghan. 2010. PS 60-137: The response of European buckthorn, Rhamnus cathartica to soil amendments in restoration. The 95th ESA Annual Meeting.

Ponge, J. F. 1991. Succession of fungi and fauna during decomposition of needles in a small area of Scots pine litter. Plant and Soil **138**:99-113.

Pouyat, R. V., and M. M. Carreiro. 2003. Controls on mass loss and nitrogen dynamics of oak leaf litter along an urban-rural land-use gradient. Oecologia **135**:288-298.

Preston, C. M., J. A. Trofymow, and t. C. I. D. E. Working Group. 2000. Variability in litter quality and its relationship to litter decay in Canadian forests. Canadian Journal of Botany **78**:1269-1287.

Prober, S. M., K. R. Thiele, I. D. Lunt, and T. B. Koen. 2005. Restoring ecological function in temperate grassy woodlands: manipulating soil nutrients, exotic annuals and native perennial grasses through carbon supplements and spring burns. Journal of Applied Ecology **42**:1073-1085.

Rack, K., and U. Scheidemann. 1987. Succession and pathogenic properties of fungi inhabiting pine needles. European Journal of Forest Pathology **17**:102-109.

Reinhart, K. O., and R. M. Callaway. 2004. SOIL BIOTA FACILITATE EXOTIC ACER INVASIONS IN EUROPE AND NORTH AMERICA. Ecological Applications **14**:1737-1745.

Reinhart, K. O., and R. M. Callaway. 2006. Soil biota and invasive plants. New Phytologist **170**:445-457.

Reza, M. I. H., and S. A. Abdullah. 2011. Regional Index of Ecological Integrity: A need for sustainable management of natural resources. Ecological Indicators **11**:220-229.

Ritz, K., H. I. J. Black, C. D. Campbell, J. A. Harris, and C. Wood. 2009. Selecting biological indicators for monitoring soils: A framework for balancing scientific and technical opinion to assist policy development. Ecological Indicators **9**:1212-1221.

Robertson, G. P., D. C. Coleman, C. S. Bledsoe, and P. Sollins. 1999. Standard soil methods for long-term ecological research. Oxford University Press.

Rodgers, V. L., B. E. Wolfe, L. K. Werden, and A. C. Finzi. 2008. The invasive species Alliaria petiolata (garlic mustard) increases soil nutrient availability in northern hardwood-conifer forests. Oecologia **157**:459-471.

Rosenfeld, J. S. 2002. Functional redundancy in ecology and conservation. Oikos **98**:156-162.

Ross, K. A., J. G. Ehrenfeld, and M. V. Patel. 2011. The effects of nitrogen addition on the growth of two exotic and two native forest understory plants. Biological Invasions **13**:2203-2216.

Rowe, H. I. 2010. Tricks of the Trade: Techniques and Opinions from 38 Experts in Tallgrass Prairie Restoration. Restoration Ecology **18**:253-262.

Ruiz-Jaén, M. C., and T. M. Aide. 2005. Vegetation structure, species diversity, and ecosystem processes as measures of restoration success. Forest Ecology and Management **218**:159-173.

Ruiz-Jaen, M. C., and T. Mitchell Aide. 2005. Restoration Success: How Is It Being Measured? Restoration Ecology **13**:569-577.

Samson, F. B., and F. L. Knopf. 1996. Prairie conservation: preserving North America's most endangered ecosystem. Island Press.

Sariyildiz, T., and J. M. Anderson. 2003. Interactions between litter quality, decomposition and soil fertility: a laboratory study. Soil Biology and Biochemistry **35**:391-399.

Scherer-Lorenzen, M. 2008. Functional diversity affects decomposition processes in experimental grasslands. Functional Ecology **22**:547-555.

Schneider, T., K. M. Keiblinger, E. Schmid, K. Sterflinger-Gleixner, G. Ellersdorfer, B. Roschitzki, A. Richter, L. Eberl, S. Zechmeister-Boltenstern, and K. Riedel. 2012. Who is who in litter decomposition? Metaproteomics reveals major microbial players and their biogeochemical functions. The Isme Journal **6**:1749.

Senthilkumar, K., K. Udaiyan, and S. Manian. 1993. Successional pattern of mycoflora associated with litter degradation in a *Cymbopogon caesius* dominated tropical grassland. Tropical Grasslands **27**:121-127.

SER, S. f. E. R. I. S. a. P. W. G., SER. 2004. The SER International Primer on Ecological Restoration.

Seto, K. C., M. Fragkias, B. Gü neralp, and M. K. Reilly. 2011. A Meta-Analysis of Global Urban Land Expansion. PLoS ONE **6**:1-9.

Shochat, E., S. B. Lerman, J. M. Anderies, P. S. Warren, S. H. Faeth, and C. H. Nilon. 2010. Invasion, Competition, and Biodiversity Loss in Urban Ecosystems. BioScience **60**:199-208.

Simberloff, D., and B. Von Holle. 1999. Positive interactions of nonindigenous species: invasional meltdown? Biological Invasions **1**:21-32.

Sinsabaugh, R. L., R. K. Antibus, and A. E. Linkins. 1991. Proceedings of the International Workshop on Modern Techniques in Soil Ecology Relevant to Organic Matter Breakdown, Nutrient Cycling and Soil Biological Processes An enzymic approach to the analysis of microbial activity during plant litter decomposition. Agriculture, Ecosystems & Environment **34**:43-54.

Smith, S. E., and D. J. Read. 1997. Myorrhizal Symbiosis. 2nd edition. Academic Press, San Diego.

Spehn, E. M., J. Joshi, B. Schmid, J. Alphei, and C. Körner. 2000. Plant diversity effects on soil heterotrophic activity in experimental grassland ecosystems. Plant and Soil **224**:217-230.

Steinberg, D. A., R. V. Pouyat, R. W. Parmelee, and P. M. Groffman. 1997. Earthworm abundance and nitrogen mineralization rates along an urban-rural land use gradient. Soil Biology and Biochemistry **29**:427-430.

Stendell, E. R., T. R. Horton, and T. D. Bruns. 1999. Early effects of prescribed fire on the structure of the ectomycorrhizal fungus community in a Sierra Nevada ponderosa pine forest. Mycological Research **103**:1353-1359.

Suding, K., K. LeJeune, and T. Seastedt. 2004. Competitive impacts and responses of an invasive weed: dependencies on nitrogen and phosphorus availability. Oecologia **141**:526-535.

Suter Ii, G. W. 2001. Applicability of indicator monitoring to ecological risk assessment. Ecological Indicators **1**:101-112.

Swift, M. J., O. W. Heal, and J. M. Anderson. 1979. Decomposition in terrestrial ecosystems. University of California Press, Berkley. CA.

Taylor, B. R., D. Parkinson, and W. F. J. Parsons. 1989. Nitrogen and Lignin Content as Predictors of Litter Decay Rates: A Microcosm Test. Ecology **70**:97-104.

Team, R. C. 2015. A Language and Environment for Statistical Computing.

Tedersoo, L., M. Bahram, S. Põlme, U. Kõljalg, N. S. Yorou, R. Wijesundera, L. V. Ruiz, A. M. Vasco-Palacios, P. Q. Thu, A. Suija, M. E. Smith, C. Sharp, E. Saluveer, A. Saitta, M. Rosas, T. Riit, D. Ratkowsky, K. Pritsch, K. Põldmaa, M. Piepenbring, C. Phosri, M. Peterson, K. Parts, K. Pärtel, E. Otsing, E. Nouhra, A. L. Njouonkou, R. H. Nilsson, L. N. Morgado, J. Mayor, T. W. May, L. Majuakim, D. J. Lodge, S. S. Lee, K.-H. Larsson, P.

Kohout, K. Hosaka, I. Hiiesalu, T. W. Henkel, H. Harend, L.-d. Guo, A. Greslebin, G. Grelet, J. Geml, G. Gates, W. Dunstan, C. Dunk, R. Drenkhan, J. Dearnaley, A. De Kesel, T. Dang, X. Chen, F. Buegger, F. Q. Brearley, G. Bonito, S. Anslan, S. Abell, and K. Abarenkov. 2014. Global diversity and geography of soil fungi. Science **346**.

Termorshuizen, A. J. 1991. Succession of mycorrhizal fungi in stands of *Pinus sylvestris* in the Netherlands. Journal of Vegetation Science, 1991. 2(4): p. 555-564. Journal of Vegetation Science **2**:555-564.

Thorpe, A. S., and A. G. Stanley. 2011. Determining appropriate goals for restoration of imperilled communities and species. Journal of Applied Ecology **48**:275-279.

Tibbett, M., F.E. Sanders, S.J. Minto, M. Dowell, and J.W.G. Cairney, . 1998. Utilization of organic nitrogen by ectomycorrhizal fungi (*Hebeloma* spp.) of arctic and temperate origin. Mycologial Research **102**:1525-1532.

Tilman, D., J. Knops, D. Wedin, P. B. Reich, M. Ritchie, and E. Siemann. 1997. The Influence of Functional Diversity and Composition on Ecosystem Processes. Science **277**:1300-1302.

Tiunov, A. V., C. M. Hale, A. R. Holdsworth, and T. S. Vsevolodova-Perel. 2006. Invasion patterns of Lumbricidae into the previously earthworm-free areas of northeastern Europe and the western Great Lakes region of North America. Biological Invasions **8**:1223-1234.

Trappe, J. M. 1977. Selection of fungi for ectomycorrhizal inoculation in nurseries. Annu Rev Phytopathol **15**.

Vačkář, D., B. ten Brink, J. Loh, J. E. M. Baillie, and B. Reyers. 2012. Review of multispecies indices for monitoring human impacts on biodiversity. Ecological Indicators **17**:58-67.

van Maanen, A., and F. Gourbiere. 1997. Host and geographical distribution of *Verticicladium trifidum*, *Thysanophora penicillioides*, and similar fungi on decaying coniferous needles. Canadian Journal of Botany **75**:699-710.

Vilà, M., J. L. Espinar, M. Hejda, P. E. Hulme, V. Jarošík, J. L. Maron, J. Pergl, U. Schaffner, Y. Sun, and P. Pyšek. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters **14**:702-708.

Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and D. G. Tilman. 1997. Human alternation of the global Nitrogen cycle: sources and consequences. Ecological Applications **7**:737-750.

Walker, B., A. Kinzig, and J. Langridge. 1999. Original Articles: Plant Attribute Diversity, Resilience, and Ecosystem Function: The Nature and Significance of Dominant and Minor Species. Ecosystems **2**:95-113.

Walker, K. J., P. A. Stevens, D. P. Stevens, J. O. Mountford, S. J. Manchester, and R. F. Pywell. 2004. The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. Biological Conservation **119**:1-18.

Weidenhamer, J. D., and R. M. Callaway. 2010. Direct and indirect effects of invasive plants on soil chemistry and ecosystem function. Journal of chemical ecology **36**:59-69.

White, P. S., and J. L. Walker. 1997. Approximating Nature's Variation: Selecting and Using Reference Information in Restoration Ecology. Restoration Ecology **5**:338-349.

White, T. A., D. J. Barker, and K. J. Moore. 2004. Vegetation diversity, growth, quality and decomposition in managed grasslands. Agriculture, Ecosystems & Environment **101**:73-84.

Wieder, R. K., and G. E. Lang. 1982. A Critique of the Analytical Methods Used in Examining Decomposition Data Obtained From Litter Bags. Ecology **63**:1636-1642.

Wilson, E. O. 1999. The diversity of life. WW Norton & Company.

Wilson, S. D., and A. K. Gerry. 1995. Strategies for Mixed-Grass Prairie Restoration: Herbicide, Tilling, and Nitrogen Manipulation. Restoration Ecology **3**:290-298.

Wohl, D. L., S. Arora, and J. R. Gladstone. 2004. Functional redundancy supports biodiversity and ecosystem function in a closed and constant environment. Ecology **85**:1534-1540.

Yelenik, S. G., W. D. Stock, and D. M. Richardson. 2004. Ecosystem Level Impacts of Invasive Acacia saligna in the South African Fynbos. Restoration Ecology **12**:44-51.

Yin, B., D. Crowley, G. Sparovek, W. J. De Melo, and J. Borneman. 2000. Bacterial functional redundancy along a soil reclamation gradient. Appl Environ Microbiol **66**:4361-4365.

Young, T. P., D. A. Petersen, and J. J. Clary. 2005. The ecology of restoration: historical links, emerging issues and unexplored realms. Ecology Letters **8**:662-673.

Zhang, D., D. Hui, Y. Luo, and G. Zhou. 2008. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. Journal of Plant Ecology **1**:85-93.

Appendix A

Chapter 1: Value added resources to region

One of the primary goals of the Chicago Wilderness Land Management Research Program (CWLMRP) or 100 Sites for 100 Years is to encourage collaborations in conservation and increase the level of applied ecological research within the region. By creating an infrastructure that facilitates partnership and collaborations among faculty, graduate students, and research institutions, the program seeks to educate the next generation of scientists in applied and urban ecology methods and scientific inquiry.

A significant hurdle for conducting research and especially graduate research is often not the limitations of compelling research questions that test and apply ecological theory, but rather the logistical challenges in determining where to conduct studies that address key ecological questions. Determining appropriate habitats, obtaining management histories and basic ecological histories, and gaining permission and permits to access and sample sites can be difficult, particularly when one considers that sites are owned by different municipalities, each with their own unique bureaucratic processes. This is further complicated when land management activities on the ground are conducted by a combination of land owner staff, private contractors, and/or volunteer stewards. The simplification and streamlining of this site identification process is therefore attractive to PIs, graduate students, and undergraduate students interested in conducting research within the region. While the inherent experimental design encourages research questions to have an applied focus on the impacts of restoration and management duration on key ecological variables, the network provides a wide range of plant community types that can be used to address questions about structure, function, and diversity relationships or ecological processes.

Since the program's inception in 2009, graduate, undergraduate, and high school students have undertaken research on the fundamental questions posed by the CWLMRP (Table 1). This involvement has promoted opportunities for the inclusion of under-represented groups in STEM, and fostered mentoring among students, especially between undergraduates and high school students. In addition, student-lead research promotes a greater variety of study organisms and ecological questions, given that a student's interest and experience may be tangential to that of their advisor. Overall, these outcomes are consistent with the goals of STEM education and research experience, a major focus of the National Science Foundation.

These partnerships have also helped to create and promote a critical mass of researchers addressing conservation challenges and opportunities in the region through presentations at academic and practitioner conferences, and outreach activities with the general public. For example, collaborators have delivered over 60 oral or poster presentations at local, national, and international conferences, have published nine peer reviewed journal articles, and four book chapters that highlight the conservation, restoration and research of the Chicago Region.

Together, these activities promote the integration of basic and applied science, and between researchers and manages. These outcomes further the goal of connecting people with natural spaces in unique ways.

Appendix A. Table 1. Collaboration and resources within the 100 Sites for 100 Years Program (last updated December, 2016).

Collaborating Institutions	17
Graduate Students	8
Research Assistants	74
High School Students	12
Presentations	62
Papers published	9
Papers in review or revision	1
Book Chapters	4
Financial support	>$719,000
Funding Sources	20

Appendix B

Chapter 3: Individual variable maps and indices

Soil N Availability

Spatial analysis indicated that these patterns were largely driven by areas of high soil N in the northwestern sites (Figure 1).

Relativized soil fertility significantly differed by management category ($F = 3.1$, $p = 0.037$) and targeted pairwise comparisons show a moderate difference between control and managed sites ($p = 0.08 - 0.10$) and no difference between managed sites ($p > 0.98$).

Earthworms

Spatial interpolation showed that there was little spatial variability in earthworm biomass even though a higher earthworm biomass was observed at the northern and southern most sampled sites (Figure 2).

Relativized earthworm biomass had no significant difference in management categories ($F = 2.7$, $p = 0.10$).

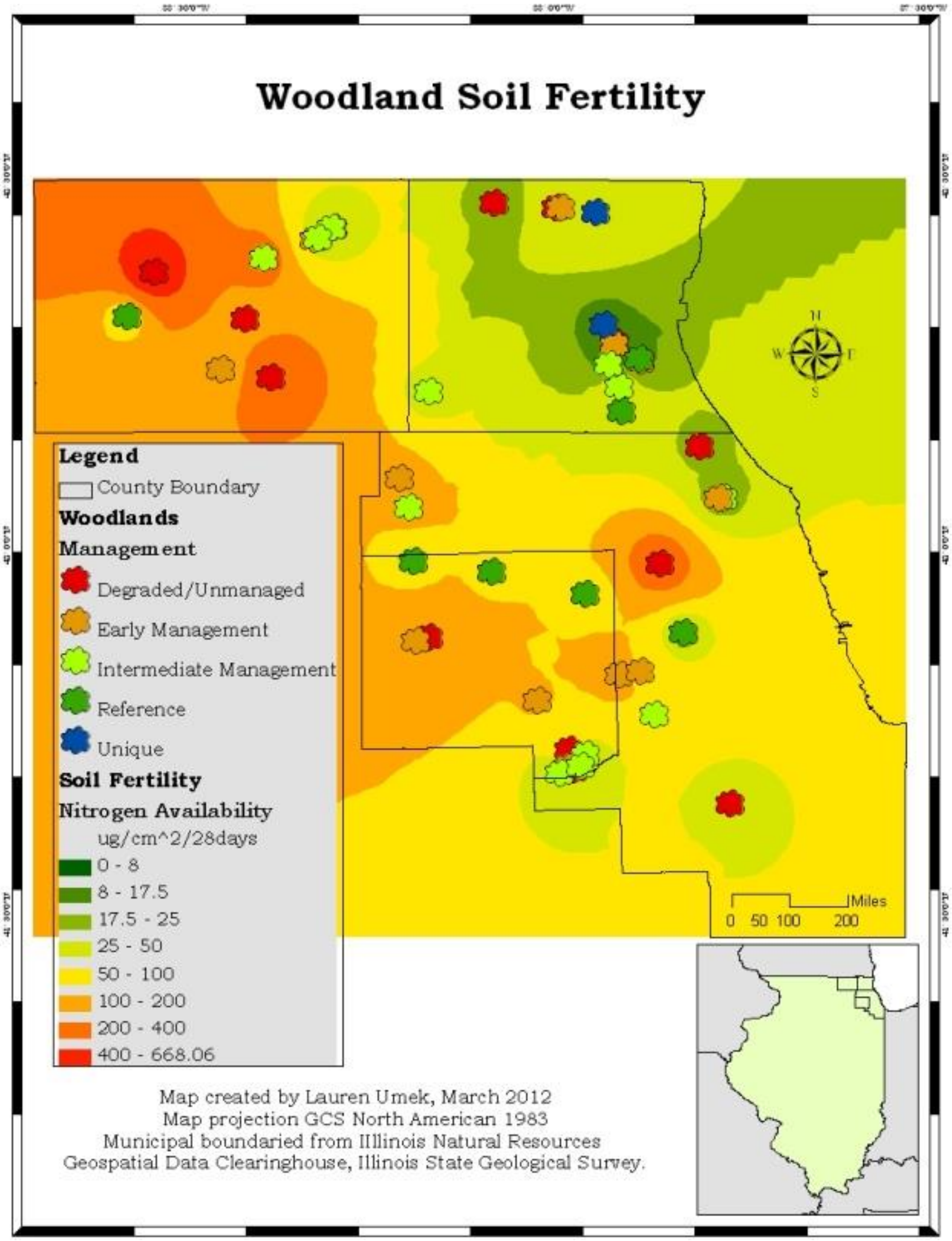
Woodland Degradation

The calculated woodland degradation index by management (Figure 4) showed similar patterns as the individual characteristics where unmanaged, control sites show greater degradation (1) than the other management categories and reference sites had the lowest (0.32).

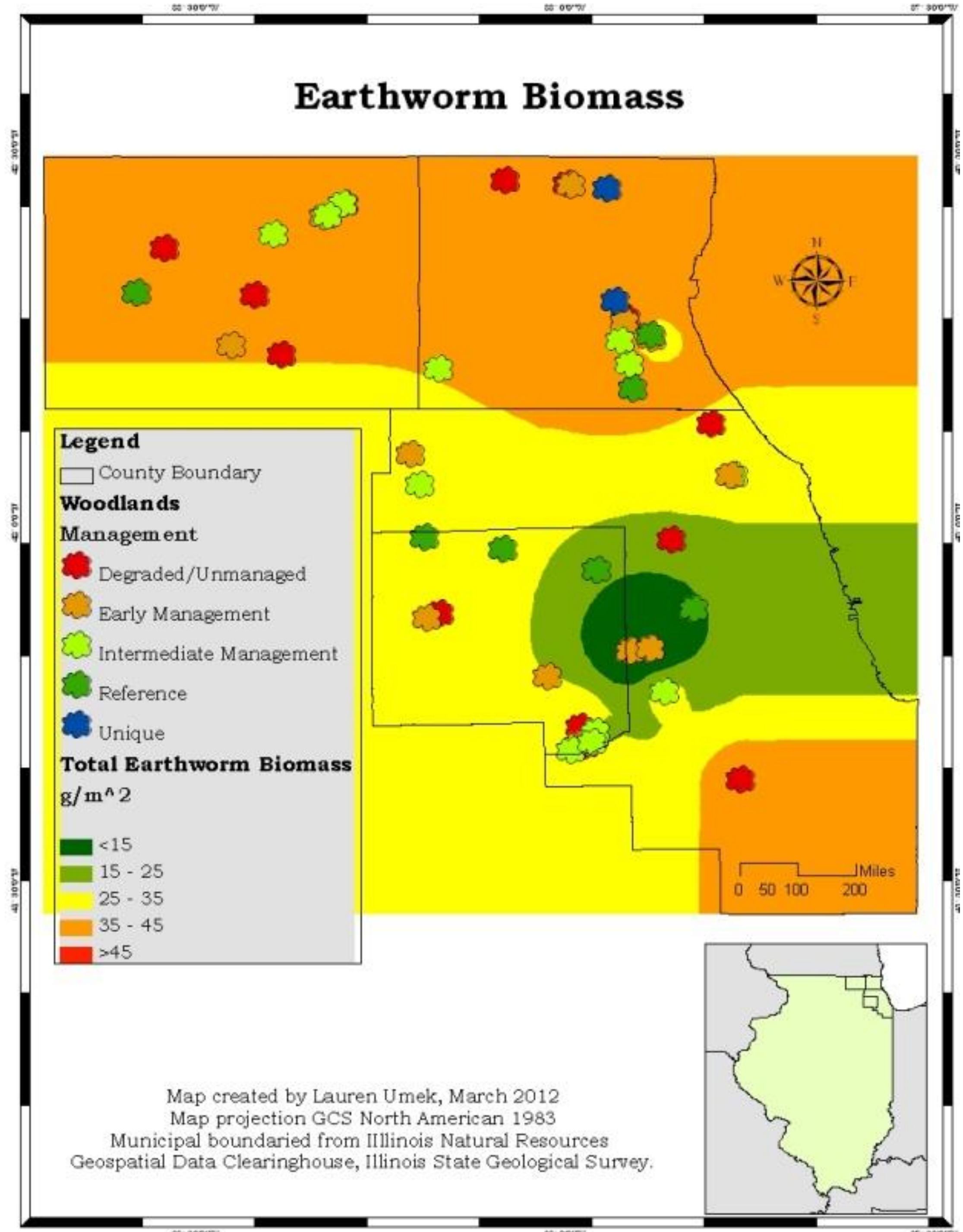
Woodland degradation index was calculated from relativized values of earthworm biomass, soil N availability and invasive shrub cover. The values for each independent response variable was divided by the maximum observed value of any site, giving each variable a range from zero to one. These values were then averaged by management category and combined management to determine an index of woodland degradation ranging from zero to one with higher numbers representing the highest mean observed value for all three response variables.

Spatial analysis insights

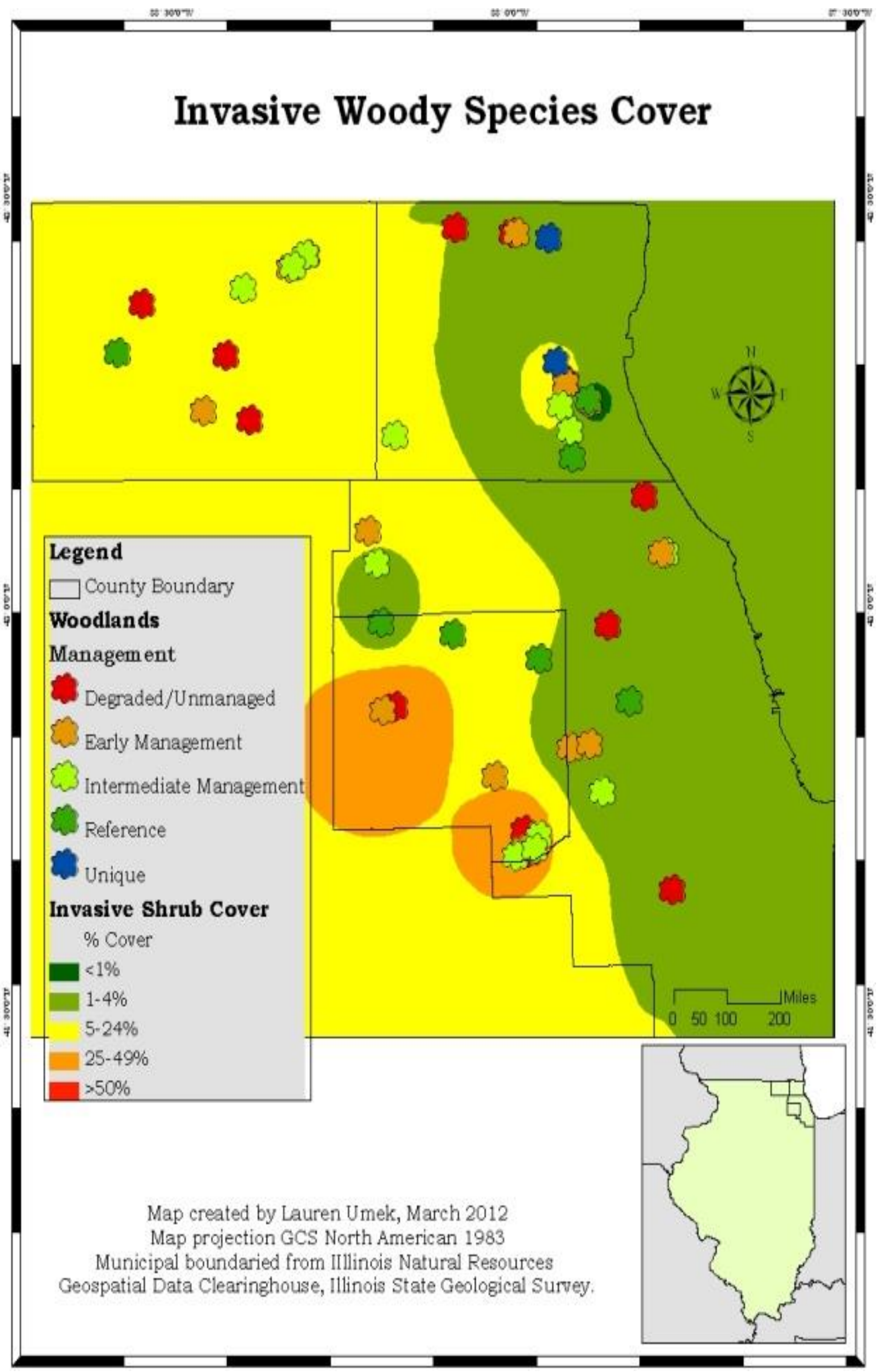
The IDW map of soil fertility also shows that McHenry County generally has higher soil N availability than the other 3 counties. While not statistically significant, ($F = 2.1$, $p = 0.1$) these differences could be because McHenry County is less developed and maintains a more rural landscape, with agricultural fields prevalent. Fertilizer use in the area is likely influencing the soil chemistry or surrounding natural areas, potentially creating current and future land management concerns. One of the intermediate managed woodlands located in McHenry county has high soil N compared to the other sites (56.4 ± 24.8 with, 33.4 ± 10.1 without; mean ± S.E. and is the only managed site in the highest 5 sites).



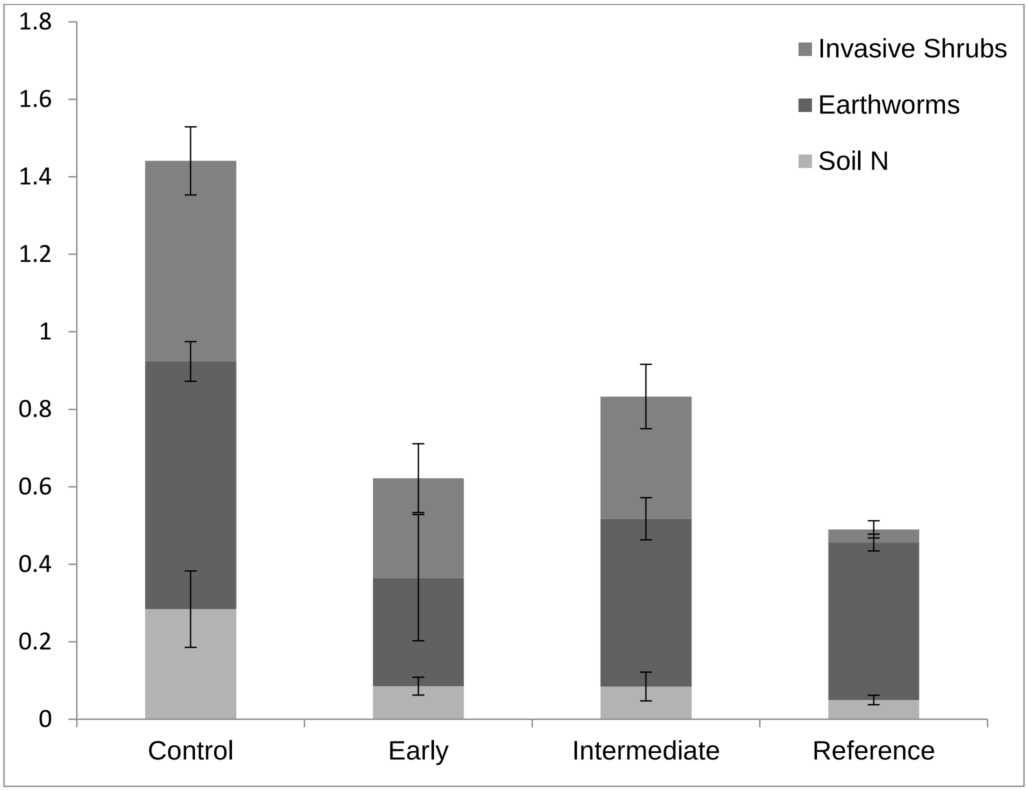
Appendix B. Figure 1: Spatial integration (IDW) of total nitrogen availability.



Appendix B. Figure 2: Spatial Interpolation of earthworm biomass



Appendix B. Figure 3: Mean cover (ordinal cover classes 0-6) of invasive woody shrubs by management category.



Appendix B. Figure 4: Index of woodland degradation on by management category.

Appendix C

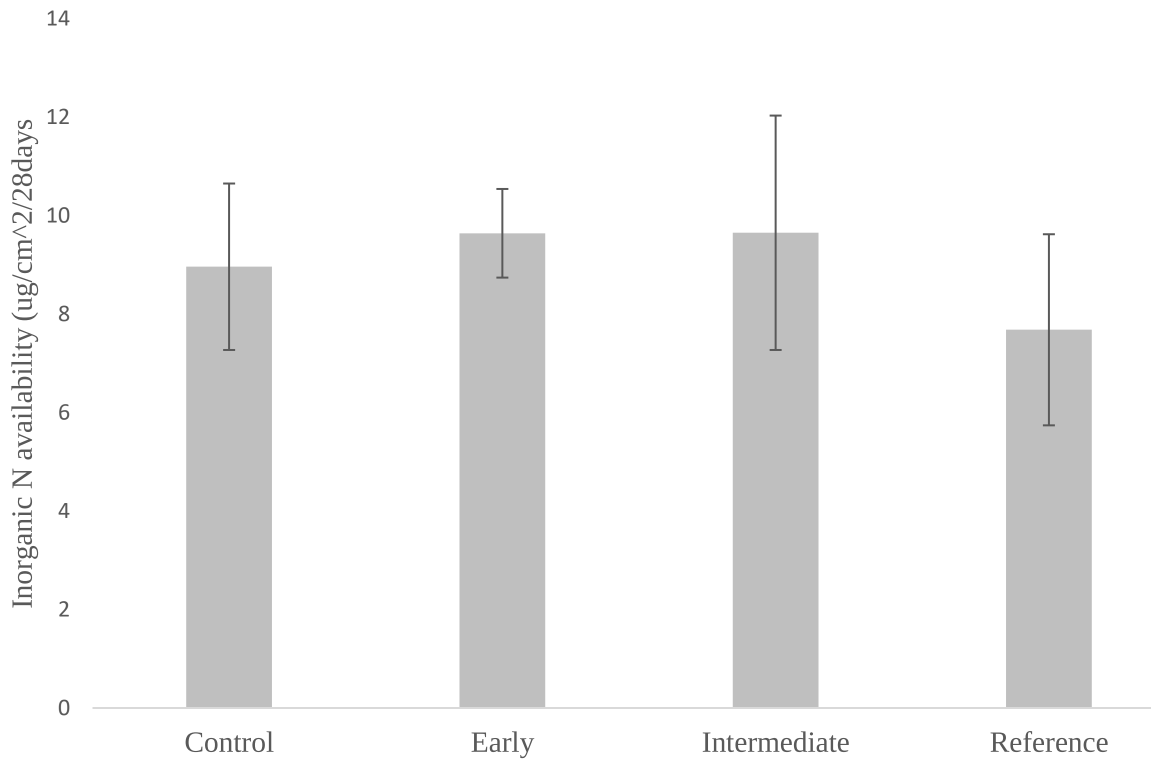
Chapter 4: Soil and vegetation cover tables and inorganic nitrogen by management

Appendix C. Table 1: Summary of soil variables by site

SiteName	Moisture	Total Inorganic N	NO3	NH4	Ca	Mg	K	P	Fe	Mn	Cu	Zn	B	S	Pb	Al	Cd	PctN	PctC	C:N
BeaubienEast	0.510	9	6.4	2.6	2892	532	15.8	3	135.2	3	7	38.2	2.4	201	30.2	32.4	0.2	0.58	8.16	14.1
BeaubienWest	0.499	9.8	5.4	4.4	2668	547.4	25.8	0.8	146.4	1.8	12.2	31.2	2.6	362	37.2	30.6	0.2	0.51	7.32	14.3
BergmanNorth	0.167	7.3	2	5.3	756	323.1	120.8	3	1.6	0.6	0.2	0.5	0.5	13	0	18.2	0	0.18	2.42	13.5
Berkeley	0.096	9.7	7.4	2.2	1750	514.2	45.8	3.5	4	2.2	0.5	1.3	0.2	29	0.6	26.4	0	0.33	3.95	12.0
CubaMarsh0	0.145	15.4	11.2	4.2	2216	465.7	38.9	16.5	45.9	19	1.5	3	0.4	197.1	3.1	29.3	0	0.46	5.79	12.7
CubaMarsh2	0.077	8.2	5.3	2.9	1887	539.5	154.8	23.7	6.7	6.3	0.6	2	0.4	71.7	1.3	30.1	0	0.51	6.45	12.6
GPPioneerN	0.027	3.2	2.2	1	2087	486.5	27.4	37.9	199.5	64.3	1	3.5	0.7	47	1.8	24.8	0	0.32	4.31	13.4
GPPioneerS	0.256	5.6	4.2	1.4	2233	592.6	24.3	27.9	11.2	1.2	0.7	1.9	0.7	24.6	0.9	26.4	0	0.28	3.56	12.9
GrantWoods2	0.109	2.6	1.2	1.4	2556	602.8	33	3.2	5.6	1.6	0.6	1	2.6	10	1	37.6	0	0.49	6.14	12.4
GrantWoods3	0.675	7.2	2.8	4.4	3040	365.4	16.2	1.8	117.6	2.4	2	11.4	3.8	91.8	6	39.6	0.2	1.08	11.87	11.0
HalfDay	0.327	20.3	10.3	10	1825	571.3	105.6	20.5	5.4	5.2	0.4	1.7	0.2	35.3	0.7	25.5	0	0.28	3.26	11.6
HHBartlet	0.201	6	3.4	2.6	2128	738.4	86.8	3.2	5	1.4	0.4	1.8	2.2	5.2	0.8	27.2	0	0.29	3.68	12.6
HHHawk	0.323	12.8	7.8	5	2240	534.8	27.8	13	784.6	62.2	4.2	8.6	3	323	3.8	30.8	0	0.36	4.14	11.5
HHNorthwest	0.172	9.2	7.4	1.8	2164	595.8	60.8	6.8	6.2	2.8	0.2	1	3.2	8.2	0.4	37.4	0	0.35	4.34	12.4
Kickapoo	0.518	9.4	3.8	5.6	2454	610.8	46.8	1.4	670.2	20	2.8	10.6	3.6	148.2	13.2	37.2	0	0.41	3.95	9.7
SmithRd	0.010	7.2	3.6	3.6	2630	536.6	11.6	1.6	6	0.6	0.4	2	2.8	28.6	1.4	30.2	0.2	0.47	5.99	12.8
Somme	0.149	14.8	13.2	1.6	3600	581.2	36	4.4	14.6	2.8	1.6	1.8	4.2	124.2	3.4	43.8	0	0.44	6.70	15.4
TedStone	0.156	9.8	4	5.8	1545	500.6	111.2	5	6.6	5.2	0.2	1	2.4	23.8	0.4	27	0	0.23	2.78	11.8
TinleyCreek	0.211	6.8	4.4	2.4	1731	500.6	139.2	3.6	5.6	2.2	0.4	1.6	1.4	18.6	0.6	25.4	0	0.49	7.02	14.3
WadsworthR	0.306	7.6	4.4	3.2	2832	621.6	36	3.6	12.4	0.8	0.6	3.4	2	28.8	2.2	26.6	0	0.54	6.32	11.7
Winfield	0.184	7.4	4.6	2.8	2082	562.8	25.4	1.8	5	0.8	0.2	1	2.6	6.4	0.4	30.2	0	0.41	5.32	13.0

Appendix C. Table 2: Summary of median vegetation functional group cover by site.

SiteName	Year Sampled	Native Grass	Non-native Grass	Native Forbs	Non-native Forbs	Woody Stems	Sedges and Rushes	Moss	Detritus	Bareground
Beaubien East	2010	4	0	4	0	3	3	1	2	2
Beaubien West	2010	3	0	5	0	3	1	1	2	2
Bergman North	2010	4	0	6	2	3	3	1	2	1
Berkeley	2011	4	0	5	0	3	4	0	6	1
Cuba Marsh R0	2011	4	2	3	3	3	0	1	4	1
Cuba Marsh R2	2011	5	3	4	2	0	0	1	5	1
GP Pioneer Rd	2010	4	0	4	0	0	0	0	1	3
GP Pioneer Rd South	2010	6	0	4	0	0	0	2	3	2
Grant Woods R2	2010	5	0	4	0	0	0	0	3	1
Grant Woods R3	2010	5	0	4	0	2	0	0	2	1
Half Day Rd	2011	6	3	3	0	0	0	0	5	1
HH Bartlet	2009	0	6	3	3	0	0	0	6	1
HH Hawk	2009	0	6	6	0	4	0	0	6	2
HH Northwest	2009	0	6	4	4	0	0	0	6	1
Kickapoo	2010	5	0	3	3	2	6	1	1	2
Smith Rd	2010	5	0	3	3	0	0	0	3	1
Somme	2010	4	0	5	0	3	1	1	3	2
Ted Stone	2010	4	0	4	0	3	1	0	2	2
Tinley Creek	2010	3	0	4	1	4	3	1	3	1
Wadsworth	2009	4	5	4	0	3	0	0	6	0
Winfield	2010	2	0	3	3	3	0	0	3	1



Appendix C. Figure 1. Average available inorganic Nitrogen (NO_3^- and NH_4^+) by management category