# A STUDY OF PLANT COMMUNITY ASSEMBLY DYNAMICS IN URBAN SYSTEMS THROUGH THE LENS OF RESTORATION ECOLOGY

By

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# A DISSERTATION

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#### PUBLIC ABSTRACT

Human land uses, including the expansion of urban areas, threaten biodiversity globally by damaging natural ecosystems and disrupting their functioning. Ecological restoration, or the process of assisting the recovery of an ecosystem that has been damaged or destroyed, has the potential to halt or reverse biodiversity loss due to urban expansion. Unfortunately, the outcomes of ecological restoration are often variable and unpredictable, and typically fall short of achieving the same levels of biodiversity and functioning as ecosystems which have not been impacted by human land uses. In this dissertation, I conducted a research program to identify and describe the drivers of variation among ecological restoration efforts within urban areas using a common plant community – prairies – a once abundant and now largely lost native plant community in the Midwestern U.S.A across each study.

Much of what we know about the factors that impact the outcomes of ecological restoration efforts is largely from work done in non-urban areas. To address this research gap, I developed two studies which work together to identify the factors that impact the outcomes of ecological restoration efforts in urban areas. The first was an observational study across previously established prairie restoration planting sites to identify how the plant communities within each site were impacted by factors that are often altered by urban expansion, such as the environmental site conditions and amount of urban land cover surrounding the planting sites, as well as restoration practices. This study revealed that variation in plant community composition among restoration plantings was related primarily to site-level factors, such as soil and local climate conditions, rather than the surrounding landscape context. I found that non-prairie species increased in richness in response to warmer local climate conditions but decreased in richness in response to soil conditions that had elevated water holding capacity, were less compacted, or sandier. Prairie species richness responded oppositely to these factors.

The second study examined how the plant communities are impacted by factors that are often altered by urban expansion when restoration practices are tightly controlled across newly established prairie restoration plantings in the Lansing, Michigan (USA) metro area. Factors that impact the arrival and establishment of prairie species within a restoration planting site may be different from those acting on already established prairie plant communities. Thus, the identification of factors which limit or enhance the success of establishment will enable restoration practitioners to improve restoration success. This study revealed that both local site

conditions as well as the amount of urban land cover in the surrounding landscape impacted plant community establishment, but like the previous study, prairie and non-prairie species responded to these factors differently. Prairie species richness and occurrence was consistently lower with increasing amount of surrounding urban land cover, whereas non-seeded species were largely shaped instead by environmental site conditions. Both studies indicate that restoration practices developed in non-urban areas can and should be extended to urban areas to better understand the impact of environmental site conditions and landscape context on plant community development, and that prairie plant communities are good candidates for this work.

Urban ecosystems face novel environmental conditions due to human land uses; one such challenge is roads and salt addition for winter road management. In my third chapter, I designed a study to test the impact of road salt deposition on newly established prairie plant communities to better understand how this novel environmental stressor impacts plant community assembly. Additionally, we tested the effects of road salt deposition on species sourced from both the Midwest and coastal populations of some prairie species as it is likely that ability to tolerate roadside salt deposition likely differs across and within species due to natural adaptations to saline conditions. There were clear effects of salt deposition on the seeded prairie plant species. Although prairie plant species were able to establish at all levels of salt deposition, even low levels of salt deposition had negative impacts which magnified at intermediate to high levels of salt deposition. These effects were not mitigated by sourcing seed from coastal populations.

Together, my findings illustrate that many of the same drivers of variation in non-urban systems are similarly drivers of variation in urban systems, but the details of these factors seem to differ. Additionally, prairie species may broadly be good candidates for future urban restoration efforts. My work contributes to the growing field of interpreting variation in urban restoration outcomes and may help guide future efforts to parse the responses of plant communities undergoing ecological restoration in urban systems going forward.

#### ABSTRACT

Human land uses, including urban expansion, threaten biodiversity globally through the alteration of natural ecosystems. Ecological restoration, or the process of assisting the recovery of an ecosystem that has been damaged or destroyed, has the potential to halt or reverse biodiversity loss due to urban expansion. Unfortunately, ecological restoration outcomes are often variable and unpredictable, and typically fall short of achieving the same levels of biodiversity and ecosystem functioning as ecosystems which have not been impacted by human land uses. In this dissertation, I conducted a research program to describe, through observational approaches, and resolve, through experimental approaches, the drivers of variation among urban restoration efforts across a common plant community – prairies – a once abundant and now largely lost native plant community in the Midwestern U.S.A.

Much of what we know about the drivers of variation in restoration outcomes comes largely from work in non-urban systems. To address this research gap, I developed two studies which work in tandem to identify drivers of variation in plant community assembly in urban ecosystems. The first was an observational study across previously established prairie restoration planting sites to identify how restoration outcomes among sites are mediated by factors related to urbanization, such as the abiotic site conditions and amount of urban land cover surrounding the planting sites, as well as restoration practices. This study revealed that variation in plant community composition among restoration plantings was related primarily to site-level factors, such as soil and local climate conditions, rather than the surrounding landscape context. I found that non-prairie species increased in richness in response to warmer local climate conditions but decreased in richness in response to soil conditions that had elevated water holding capacity, were less compacted, or sandier. Prairie species richness responded oppositely to these factors.

The second study examined how restoration outcomes are mediated by factors related to urbanization when restoration practices are tightly controlled across newly established prairie restoration plantings in the Lansing, Michigan (USA) metro area. Drivers of variation related to the arrival and establishment of target species within a restoration planting may be different from those acting on already established planting sites. Thus, the identification of factors which limit or enhance the success of establishment will enable restoration practitioners to improve restoration outcomes. This study revealed that both local site conditions as well as the amount of urban land cover in the surrounding landscape impacted plant community establishment, but like

the previous study, prairie and non-prairie species responded to these factors differently. Prairie species richness and occurrence was consistently negatively correlated with increasing amounts of surrounding urban land cover, whereas non-seeded species were largely shaped instead by local site conditions. Both studies indicate that restoration practices developed in non-urban areas can and should be extended to urban contexts to better understand the impact of local site conditions and landscape context on plant community development, and that prairie plant communities are good candidates for this work.

Urban ecosystems face novel environmental conditions due to human land uses; one such challenge is roads and salt addition for winter road management. In my third chapter, I designed a study to test the impact of road salt deposition on newly established prairie plant communities to better understand how this novel abiotic stressor impacts plant community assembly. Additionally, we tested the effects of road salt deposition on both Midwest and coastally sourced genotypes of some seeded species as it is likely that ability to tolerate roadside salt deposition, likely differs across species and among genotypes within species, due to natural adaptations to saline conditions. There were clear effects of salt deposition for plant community establishment and on the seeded prairie plant species. Although prairie plant species were able to establish at all levels of salt deposition, even low levels of salt deposition had negative impacts which magnified at intermediate to high levels of salt deposition. These effects were not mitigated by sourcing seed from coastal populations.

Together, my findings illustrate that many of the same drivers of variation in non-urban systems are similarly drivers of variation in urban systems, but the details of these factors seem to differ. Additionally, prairie species were largely insensitive to the gradients in local site conditions and surrounding landscape context measured thus may be good candidates for future urban restoration efforts. My work contributes to the growing field of interpreting variation in urban restoration outcomes and may help guide future efforts to parse the responses of plant communities undergoing ecological restoration in urban systems going forward

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#### <span id="page-8-1"></span>**Resolving variable restoration outcomes**

The destruction and degradation of natural ecosystems through human land use threatens biodiversity globally (Cardinale et al., 2012). Ecological restoration has the potential to halt or reverse this biodiversity loss in human impacted ecosystems, but ecological restoration outcomes are variable and often fall short of achieving the same levels of biodiversity and ecosystem functioning as intact ecosystems (Atkinson et al., 2022; Brudvig & Catano, 2021; Rey Benayas et al., 2009). This variation impedes our ability to compare outcomes across restoration efforts, refine approaches to those that are more reliably successful, or inform predictive capabilities. A major challenge to interpreting variable restoration outcomes across restoration efforts is the large number of factors, ranging from local site conditions to the ecological restoration practices, that can result in context dependencies. Resolving drivers of variation in restoration outcomes, and promoting a diverse community dominated by target species, is thus a central goal of restoration science (Brudvig et al., 2017).

We can make progress on resolving variable restoration outcomes by understanding the drivers of establishment and assembly of both target (desired) and non-target (undesired) species within restored areas. Previous work has found that these processes are frequently mediated by the local site conditions (MacDougall et al., 2008; Stuble et al., 2017; Young et al., 2015), landscape context (Crouzeilles et al., 2016; Woodcock et al., 2010), and the details of the ecological restoration practices (Brudvig & Damschen, 2011; Grman et al., 2013; Guiden et al., 2021). However, the relative importance of each of these suites of factors remains unresolved for most systems and likely vary across systems and time. To resolve drivers of variation within the context of ecological restoration, and better understand the context dependencies which may be influencing the establishment and assembly processes structuring both the target and non-target species, new research is needed (Brudvig et al., 2017).

### <span id="page-8-2"></span>**Ecology of Urban Areas**

Urbanization is a prominent force in the destruction and degradation of natural ecosystems globally (Newbold et al., 2015) and this has major impacts on the structure and function of natural ecosystems as well as the ecosystem services that they provide. Further, urban areas such as cities are often located in regions with not only high human population density but

also both high geographic and species diversity with high species endemism (Cincotta et al., 2000; Kühn et al., 2004; Luck, 2007). Thus, the resulting degradation of environmental conditions, alteration of landscape structure, and the introduction of non-native species (Kaye et al., 2006; Klaus & Kiehl, 2021; Vilà et al., 2010) as a result of continued human population growth and urbanization within these areas of high biodiversity may have an outsized effect on the structure and function urban ecosystems. Consequently, there is growing interest in conserving and restoring urban ecosystems to promote native biodiversity and ecosystem functionality (Dearborn & Kark, 2010; Nilon et al., 2017), and ecological restoration in urban systems is critical to improving our understanding of how best to meet global restoration goals as we enter the UN Decade in Ecosystem Restoration (2021-2030). Yet, our understanding of restoration ecology, which has come largely from work within non-urban environments, may not be sufficient for addressing novel challenges to urban ecosystems. Thus, how best to support and restore the biodiversity of urban ecosystems remains an open question (Rega-Brodsky et al., 2022).

We might expect similar types of factors to drive variation in restoration outcomes in urban and non-urban systems, like the local site conditions and landscape context. However, the ways in which these factors are modified by humans in the urban environment may differ and consequently, how they influence restoration outcomes may also differ. For example, urbanization alters local abiotic site conditions, such as the climate and soil conditions, which reduces the capacity of the urban environment to support target native plant communities (Kaye et al., 2006; Threlfall et al., 2016; Walker et al., 2009). Urban development features high levels of impervious surface cover, like roads and buildings, which retain heat, thus the construction of buildings and other infrastructure leads to consistently higher air temperatures in cities (i.e., the urban heat island effect (Debbage & Shepherd, 2015; Y. Li et al., 2020; Oke, 1982)). Additionally, urban soil properties are affected by urban development through the sealing of soils (i.e. coverage by impervious surface; Scalenghe & Ajmone-Marsan, 2009), damage to the soil structure through compaction via heavy machinery (Pavao-Zuckerman, 2008), as well as increases in heavy metal concentration and soil nutrient composition as a result of pollution deposition and soil amendment application (Z. Li et al., 2013; Pouyat & McDonnell, 1991). Increased air temperatures and degraded soil conditions can both result in the poor establishment and persistence of target species within a restoration setting (e.g., Czaja et al., 2020; Sullivan et

al., 2009). However, there has been little work done to understand how these local scale factors, modified through urban development, structure variation in restoration outcomes among restoration sites in urban contexts (Rega-Brodsky et al., 2022).

The landscape context surrounding urban green spaces may also differ from non-urban areas given the high proportion of human land uses and impervious surface cover. Changes in land use and landscape context due to urban development leads to habitat degradation, fragmentation, and loss at rates higher than that of non-urban areas (Liu et al., 2016) creating a heterogeneous landscape of greenspace and hardscape. Fewer high quality habitat patches and increasing distance between them will lead to impairment in species' dispersal and establishment abilities in urban areas, thus limiting the assembly of native plant communities in urban areas. However, there is a paucity of studies examining how the urban landscape context impacts community assembly within urban greenspaces (Aronson et al., 2016), and even less work has been done to understand how urban landscape context influences urban ecological restoration efforts (Rega-Brodsky et al., 2022).

The fields of restoration and urban ecology both need to move towards a more mechanistic understanding of what is driving ecological patterns and processes in cities so that we can support and restore native plant communities in urban areas (Piana et al., 2019). In this dissertation, I conducted a research program to describe, through observational approaches, and resolve, through experimental approaches, the drivers of variation among urban restoration efforts. In my second chapter, I conducted an observational study across urban prairie restoration plantings to identify how restoration outcomes among sites are mediated by factors related to urbanization and restoration practices. In my third chapter, I conducted a complimentary experimental test of how restoration outcomes are mediated by factors related to urbanization when restoration practices are tightly controlled across plantings. In my fourth chapter, I conducted an experimental test of how a specific abiotic stressor in urban areas, road salt application for winter road management, mediates restoration outcomes as well as a potential seed sourcing management tool to cope with increased urban salt loads. For each of these studies I used a common plant community – prairies – a once abundant now largely lost native plant community in the Midwestern U.S.A.

#### <span id="page-11-0"></span>**Study System**

Throughout my dissertation work, I use native tallgrass prairie plant communities as a model system. Prairie plant communities are typically defined by their dominance of grasses and forbs and the absence or scarcity of woody plant species (Weaver, 1954). Prairie plant communities historically developed and maintained due to climatic conditions (i.e., large fluctuations in seasonal temperatures and precipitation), grazing by large herbivores, and fire (Kost et al., 2007; Weaver, 1954). Prairies were once a dominant plant community type in the Midwest, extending from north-central Canada down through Texas and ranging from the foothills of the Rocky Mountains to east of the Mississippi River (Weaver, 1954). Tallgrass prairies were most commonly found on the eastern edge of the historic prairie range and are thus the most common prairie community type found in the Michigan region in which these studies are situated (Chapman & Brewer, 2008). Tallgrass prairies once covered 170 million acres but have now been reduced to less than 4% of their historic range due to conversion of land for agriculture, cattle grazing, and urban development; with most large, continuous tracts of prairie absent from the landscape by the 1930s (Kindscher & Tieszen, 1998; U.S. National Park Service, 2022). As a result, prairie plant communities have become regionally rare and thus a target plant community in the Midwest region for restoration efforts (Lenhart & Smiley 2018).

Due to the widespread loss of prairie ecosystems across the Midwest, prairie plants are uncommon in the landscape as well as rare in the soil seed bank and unlikely to naturally recolonize most proposed restoration sites (Kiehl et al., 2010; Thompson et al., 1998; Young et al., 2005). Thus, prairie restoration efforts typically rely on sowing seeds of native prairie plants and subsequently managing through mowing, herbicide, prescribed fire, and/or other methods (Mutel & Packard, 1997).

The early focus on prairies within the field of restoration ecology likely stemmed not only from their iconic nature as a previously dominant ecosystem, but also because of the accessibility of prairie restoration practices which utilize common agricultural tools like plows (Lenhart & Smiley 2018). However, ecological restoration has primarily been conducted in the rural landscape context and the findings may not extend to urban ecosystems which have a distinct biogeochemistry (Kaye et al., 2006), increased human modification of the landscape, and limits on prairie management tools (i.e., limited ability to incorporate grazers or fire). Even so, prairie plant communities have been proposed as a candidate plant community type for restoration

efforts in urban areas as urban grasslands like parks, lawns, and similar urban greenspace types have the potential to improve landscape connectivity, increase biodiversity, and enhance ecosystem services in urban centers through ecological restoration (Klaus, 2013).

#### <span id="page-12-0"></span>**Chapter 2: Drivers of urban restoration outcomes**

A systematic study of the variation in urban restoration outcomes, and the potential local and landscape scale factors which may be driving this variation, is largely absent from the literature. However, studies such as these are critical for developing reliably successful urban restoration practices. To address this knowledge gap, in Chapter 2 I surveyed 30 urban prairie restoration plantings across southern Michigan, USA. I collected plant community and site condition data (e.g., soil attributes) and quantified landscape context as the percentage of urban land surrounding each site. Variation in plant community composition among restorations was related primarily to site-level factors, such as soil compaction, texture, and water holding capacity, rather than landscape context. Non-prairie species were structured primarily by the local site conditions. There was an increase in non-prairie richness for sites that experienced warmer local climate conditions, while there was a decrease in non-prairie richness for sites where soils were less compacted, sandier, and had elevated water holding capacity. Prairie species richness responded oppositely. Overall, this chapter revealed specific factors structuring restoration outcomes in urban contexts and illustrated the importance of local site conditions, not surrounding landscape context, for shaping plant community composition. Restoration practices developed in non-urban areas should be extended to urban contexts to better understand the impact of local site conditions on plant community development.

#### <span id="page-12-1"></span>**Chapter 3: Drivers of establishment in urban restoration contexts**

Chapter 3 further identifies drivers of variation in restoration outcomes which may be stemming from limitations to the arrival and establishment of target seeded and non-target nonseeded species at a restoration site. Successful establishment of target species is crucial for restoration success; the identification of factors which limit or enhance success for target species will enable restoration practitioners to match species to restoration sites that they are best suited to which will improve restoration success while also minimizing cost (Grman et al., 2015). However, arrival and establishment of target species can be limited by the local site conditions and the surrounding landscape context, thus disentangling the effects of site-specific establishment limitations from those related to dispersal or the restoration practices remains a

persistent challenge (but see Groves & Brudvig, 2019; Stuble et al., 2017).

In Chapter 3, I established 35 small-scale prairie plantings across the Lansing, MI, USA metro area using consistent restoration practices. Often ecological restoration efforts deploy varied methods, creating challenges when trying to compare outcomes across restoration plantings. Controlling this major axis of variation allows me to better tease apart how local and landscape scale factors impact restoration outcomes. I monitored plant community composition, the richness and cover of target and non-target plant species, and individual species responses over two growing seasons. I then related community and individual species responses to the local abiotic site conditions and the surrounding landscape context of each planting site. I found that overall, several of the hypothesized local and landscape scale factors impacted plant community establishment. Canopy conditions as well as the amount of urban land cover shaped the plant community at large, with many of results playing out at the individual species level. Seeded species richness and occurrence was consistently negatively correlated with increasing amount of surrounding urban land cover, whereas non-seeded species were largely shaped instead by local scale factors like canopy and soil conditions. This chapter indicates that many of the target seeded species are relatively insensitive to the gradients in the local site conditions measured, indicating that prairie plant communities may indeed by good candidates for urban restoration efforts. However, this chapter also found that the establishment of plant communities dominated by the target plant community may require careful consideration of the local site conditions, such as the canopy and soil conditions, to control the non-seeded plant community.

#### <span id="page-13-0"></span>**Chapter 4: Novel stressor in urban restoration contexts**

The United States has an extensive road network connecting urban areas; about 20% of the total land in the U.S. is within 100 meters of a road (Riitters & Wickham, 2003) and in most places in the coterminous U.S. the next nearest road is less than 35 km away (Watts et al., 2007). This dense road network results in a challenging environment and altered ecology for many species (Coffin, 2007), including native plant communities, especially in regions where de-icing salts are applied seasonally for winter road management. Despite this, there has been increasing interest in roadside native plant community restoration as a potential method to ameliorate the detrimental effects of road pollution, restore connectivity between green spaces in urban areas, and enhance ecosystem services (Haan et al., 2012). Ecological restoration of roadside vegetation is hindered by the ability of the target plant community to tolerate the hot, dry, and salty

environmental conditions of roadsides. Native plant species, such as those found in tallgrass prairies have been proposed as candidates for roadside restoration work as they are predominately herbaceous and pose little risk to vehicle traffic (Riley & Wilkinson, 2007). However, it is unlikely that tallgrass prairie communities in the Midwest have had exposure to salt deposition similar to that of roadsides, thus it is likely that establishment will be hindered in salt impacted roadside soils. But the ability to tolerate roadside soil conditions, particularly the presence of deicing salts, likely differs across species. Yet, there has been little work done to parse the effect of road salt on the germination and establishment of native species targeted during roadside restorations (but see Blanchard et al., 2023).

In my fourth dissertation chapter, I experimentally investigated the effects of winter road salt application on the emergence and establishment of roadside plant communities. This chapter went a step further to investigate a possible management tool by testing the effects of road salt concentration on both Midwest and coastally sourced genotypes of some seeded species, which may be adapted to higher salt concentrations due to increased salt deposition in coastal regions. Overall, the plant community, seeded species, and seeded species sourced from coastal regions were all negatively impacted by all levels of salt deposition. This chapter illustrates that current ecological restoration methods are not suitable for roadside restoration efforts, and that new methods will need to be developed to establish native plant communities along road networks.

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## <span id="page-20-0"></span>CHAPTER TWO: LOCAL SITE CONDITIONS, NOT LANDSCAPE CONTEXT, INFLUENCE RESTORED PLANT COMMUNITIES IN URBAN CONTEXTS

The work presented in this chapter is part of the final publication:

Conway, E. E., & Brudvig, L. A. (2024). Local site conditions, not landscape context, influence restored plant communities within urban contexts. *Restoration Ecology*, e14109.

#### <span id="page-20-1"></span>**Abstract**

Restoration outcomes are variable, which impairs our ability to plan projects, meet goals, and predict restoration outcomes. Understanding the drivers of this variation is an important research need, especially within urban ecosystems, which support altered abiotic and biotic conditions and face higher rates of loss and degradation than non-urban areas. Despite the importance of urban areas for restoration, research and practice have largely focused on nonurban areas. It is unclear if we can extend current knowledge from restoration ecology to urban systems. Here, I surveyed 30 urban prairie restoration plantings across southern Michigan. I collected plant community and site condition data (e.g., soil attributes) and I quantified landscape context as the percentage of urban land surrounding each site. Variation in plant community composition among restorations was related primarily to site-level factors, such as soil compaction, texture, and water holding capacity, rather than landscape context. Non-prairie species were structured primarily by the local site conditions. There was an increase in nonprairie richness for sites that experienced warmer local climate conditions, while there was a decrease in non-prairie richness for sites where soils were less compacted, sandier, and had elevated water holding capacity. Prairie species richness responded oppositely. Overall, this chapter revealed specific factors structuring restoration outcomes in urban contexts and illustrated the importance of local site conditions, not surrounding landscape context, for shaping plant community composition. Restoration practices developed in non-urban areas should be extended to urban contexts to better understand the impact of local site conditions on plant community development.

#### <span id="page-20-2"></span>**Introduction**

Restoration outcomes are notoriously variable, which in turn limits our ability to plan restoration projects, reliably meet restoration goals, and predict restoration outcomes across systems (Brudvig & Catano, 2021). As a result, restored areas, on average, fall short of achieving

the same levels of biodiversity and ecosystem functioning that we observe in intact ecosystems (Atkinson et al., 2022; Rey Benayas et al., 2009). We do not understand which drivers of variation are consistently important across restoration contexts. Consequently, resolving these drivers among restored areas is an important research need for the field generally (Brudvig et al., 2017), and so that we can counter widespread declines in biodiversity and ecosystem functioning globally (Suding, 2011). However, much of the focus of past research attempting to identify consistent drivers of variation among restored areas has been limited to studies within non-urban contexts, with very little work done to understand the drivers of variation within urban contexts (Rega-Brodsky et al., 2022).

Over the past 20 years, urban land cover has increased by 50% globally (Potapov et al., 2022), resulting in a massive conversion of greenspace to hardscape. Cities are often located in naturally species-rich regions (Cincotta et al., 2000; Kühn et al., 2004; Luck, 2007), or biodiversity hotspots, thus the resulting degradation of environmental conditions, alteration of landscape structure, and the introduction of non-native species (Kaye et al., 2006; Klaus & Kiehl, 2021; Vilà et al., 2010) as a result of urbanization may have an outsized effect on urban ecosystems. Consequently, there is growing interest in conserving and restoring urban ecosystems to promote native biodiversity and ecosystem functionality (Dearborn & Kark, 2010; Nilon et al., 2017). Yet, how to best reach these goals through ecological restoration remains an open question.

The establishment and assembly of both target (desired) and non-target (undesired) species within restored areas is frequently mediated by the abiotic and biotic site conditions (MacDougall et al., 2008; Stuble et al., 2017; Young et al., 2015), landscape context (Crouzeilles et al., 2016; Woodcock et al., 2010), and the details of the ecological restoration practices (Brudvig & Damschen, 2011; Grman et al., 2013; Guiden et al., 2021). However, the relative importance of each of these suites of factors is not consistent across systems. In non-urban contexts, ecological restoration of the target plant community within degraded sites, such as grasslands that have been converted for agricultural use, is often limited by target species' ability to establish given the altered soil conditions and competition with non-target, weedy species (Gornish & Ambrozio dos Santos, 2016). Shifts in the surrounding landscape structure, like the expansion of farmlands in non-urban areas, can impact the assembly of restored plant communities by reducing sources of target species and limiting their dispersal through

fragmentation (Brudvig & Damschen, 2011; Minor et al., 2009). Ecological restoration practitioners often attempt to ameliorate the impact of altered site conditions and landscape contexts by implementing management practices such as seeding target species to overcome dispersal limitations, removing undesired species, or amending soils, but these approaches vary from site to site, which can also introduce variation in restoration outcomes (Grman et al., 2013; Guiden et al., 2021; Meissen et al., 2020). Current understanding of how local and landscape factors structure restoration outcomes is derived primarily from non-urban systems, with very little work done to examine these drivers in urban systems.

We would expect similar types of factors to drive variation in restoration outcomes in urban systems as in non-urban, such as the biotic and abiotic site conditions, landscape context, and restoration practices implemented. However, the ways in which these factors are modified by humans in the urban environment may differ and consequently, how they influence restoration outcomes may also differ. Previous work has found that urbanization – often quantified as impervious surface cover – modifies biodiversity. High levels of urbanization, or greater than 50% impervious surface cover, result in a decrease in overall species richness (McKinney, 2008; Rega-Brodsky et al., 2022). Moderate levels of urbanization, between 20-50% impervious surface cover, tend to support non-native species assemblages of varying diversity among different taxonomic groups (McKinney, 2008; Rega-Brodsky et al., 2022). Novel, nontarget species assemblages found in urban environments may compete with target species during restoration and reduce target species establishment (Johnson & Handel, 2016; Shochat et al., 2010). Further, urbanization alters local abiotic site conditions, which reduces the capacity of the urban environment to support target native plant communities (Threlfall et al., 2016; Walker et al., 2009). Abiotic site conditions including local climate and soil conditions are altered by urban development (Kaye et al., 2006). For instance, the urban climate is modified by the presence of impervious surfaces like pavement, buildings, and other infrastructure, which can lead to consistently higher air temperatures in cities (i.e., the urban heat island effect (Li et al., 2020; Oke, 1982)). These high temperatures can increase heat stress related mortality of urban plants (Czaja et al., 2020); this, in turn, may reduce plant establishment or persistence during restoration. Urban soils may be impacted by a legacy of urban development through damage to the soil structure via compaction from construction machinery (Pavao-Zuckerman, 2008) and increases in heavy metal concentration from pollution deposition which can alter soil chemistry

(Pouyat & McDonnell, 1991). Studies of the impact of local site conditions on restoration outcomes within urban contexts are limited. However, soil compaction has been found to lead to lower target species richness in urban restoration plantings (e.g., Sullivan et al. 2009).

Urban landscapes are composed of mosaics of different land uses (Niemelä, 1999), including housing developments, transportation infrastructure, highly managed green spaces such as parks or golf courses, and remnant natural areas. Surrounding landscape context of urban greenspaces can affect local biodiversity by inclusion of impervious surfaces like roads that can facilitate the movement of invasive species (Skultety & Matthews, 2017) and reduce dispersal and recruitment abilities of native species (Overdyck & Clarkson, 2012), and by influencing human recreational use of urban greenspaces (Talal & Santelmann, 2019). However, the ways in which cities develop, and prioritize green space within a city, varies from city to city. Further, there is a paucity of studies examining how the urban landscape context impacts community assembly within urban greenspaces (Aronson et al., 2016), and even less work has been done to understand how urban landscape context influences urban ecological restoration efforts (Rega-Brodsky et al., 2022).

If the ways in which local and landscape factors impact restoration outcomes differ between urban and non-urban areas, but the same general types of factors explain variation, we may be able to translate our current understanding of restoration ecology to urban systems. For instance, the abiotic site conditions, specifically highly compacted soils due to construction with heavy machinery, may impair target species establishment at a site. Though the cause of compaction may be different, the ecological restoration practices developed to cope with similar conditions in former agricultural fields or mining sites may be transferable to the urban environment. However, if new types of factors are important, a new urban ecological restoration framework may be needed. For example, if urban areas are experiencing consistently higher temperatures and related climate modifications due to the urban heat island effect, this may result in a mismatch between the regional climate conditions that species are adapted to and urban climate conditions, impairing target species establishment at a site. This may suggest the need for new restoration approaches in urban areas, such as the use of seed mixes containing novel species assemblages or genotypes.

To identify potential drivers of variation in urban restoration outcomes which may be structuring plant community variation, I posed a series of questions: How do local and landscape

factors, specifically local site conditions, landscape context, and restoration practices structure restored plant communities? How do prairie and non-prairie species respond to these local and landscape factors? And how do these findings in urban contexts align with our understanding gained from studies conducted in non-urban contexts? To do this, I surveyed 30 urban prairie restoration plantings across three cities in southern Michigan, USA. I hypothesized that localscale abiotic site conditions such as soil attributes (e.g., soil texture, nutrient content, soil water holding capacity), canopy cover, local climate conditions (e.g., seasonal and annual variation in temperature and precipitation), restoration practices, and landscape context quantified as the percentage of urban land surrounding each site, contribute to variation in plant communities among sites undergoing restoration in urban contexts. I explored their roles across the plant communities of these planting sites, with a focus on plant species that are the target of restoration (prairie species) and those that are not (non-prairie species).

#### <span id="page-24-0"></span>**Methods**

#### <span id="page-24-1"></span>*Study System*

I conducted this study within urban, restored prairie plant communities. Prairie plant communities are typically defined by their dominance of grasses and forbs and the scarcity of woody plant species (Weaver, 1954). Prairies were once a dominant community type throughout the Midwestern U.S., covering nearly 70 million hectares, and were once abundant in southern Michigan, where this study was situated (Chapman & Brewer, 2008; Cohen et al., 2021). However, prairies have now been reduced to less than 4% of their historic range within the U.S. due to conversion of land for agriculture, cattle grazing, and urban development (Kindscher & Tieszen, 1998; U.S. National Park Service, 2022). Prairie plant communities have become regionally rare as a result and are a common target for restoration efforts (Lenhart & Smiley 2018). Further, prairie plant communities have been proposed as a candidate plant community type for restoration efforts in urban areas as urban grasslands like parks, lawns, and similar urban greenspace types have the potential to improve landscape connectivity, increase biodiversity, and enhance ecosystem services in urban centers through ecological restoration (Klaus, 2013). *Study Design*

<span id="page-24-2"></span>This study assessed the restoration outcomes for each prairie planting site, considering community composition, richness of the entire plant community, as well as prairie and nonprairie species richness and cover. I focused this study on three urban centers in southern

Michigan, Ann Arbor, Grand Rapids, and Kalamazoo. I chose these three cities because they are within the top 20 largest in Michigan based on population size, ranging from 196, 908 in Grand Rapids to 72,873 in Kalamazoo (QuickFacts 2020), and because each has a notable number of urban prairie restoration plantings. For each city, I first populated a list of potential prairie restoration study sites based on discussions with local restoration practitioners and park managers. From this list, I included sites in this study if I were able to identify a contact person for site access, the site was reconstructed through seed sowing (i.e., not remnants undergoing management), the site resembled a prairie based on a ground truthing visit (i.e., there was not significant woody encroachment), and if land managers retained information about planting site age and total seeded area. I did not impose a minimum distance between sites to maximize the number of planting sites which could be included in this study and sampled every site on our list that met these criteria. The minimum distance between plots was 91 meters, and the average study site was approximately 8 acres (site size ranged from 0.05 – 14.5 hectares). In total, I included 30 prairie plantings in this study: 12 in Ann Arbor, 12 in Grand Rapids, and 6 in Kalamazoo (Fig 2.1). I collected data on local and landscape factors within each site in addition to plant community composition data within five,  $1\times1$ -meter subplots along a central, randomly oriented 20 meter transect in each of the 30 planting sites June-August 2020. I recorded the cover of each plant species as the percentage of the subplot occupied by each species present. *Site Conditions, Landscape Context, & Restoration Practices Data Collection*

<span id="page-25-0"></span>Site conditions in this study included site age, tree canopy cover, soil conditions, and bioclimatic conditions. I defined site age as the number of growing seasons since a restoration was initiated by sowing seeds of native prairie species. I collected canopy cover and soil condition data at each of the five subplots within each planting site. The canopy cover was measured at the same corner of each of the five subplots within each planting site using a spherical crown densiometer. Values were then averaged across the subplots to generate one value for each planting site. I determined soil conditions by measuring soil texture (the percent of sand, silt, and clay) using the LaMotte Soil Texture test kit, depth to soil compaction (depth in cm to 300 PSI) using a Dickey-John Soil Compaction Tester, soil water holding capacity (calculated as the proportional difference between the wet and dry weight of the soil samples using the methods laid out in Brudvig & Damschen 2011), and soil nutrient composition. I sent soil samples to Brookside Laboratory, Inc. for soil nutrient testing (Soil Test: Standard Soil with

Bray I P). I defined bioclimatic conditions as seasonal and annual temperature and precipitation metrics which influence local-scale prairie plant community establishment and abundance (Groves et al. 2020) such as mean summer and winter precipitation and temperature as well as the fluctuation between summer and annual temperatures. To do this, I generated 19 bioclimatic variables (Hijmans et al. 2005) from 800m resolution PRISM (PRISM Climate Group) monthly temperature and precipitation data ranging from the year of planting site establishment until December 2020, the year of our survey.

I quantified landscape context as the percentage of developed land within a 500m radius of each site by using ArcGIS Pro software and land use/landcover maps produced by the National Land Cover Database (NLCD) Landcover & Imperviousness for 2019 (Dewitz & U.S.G.S 2021) The NLCD Landcover & Imperviousness maps include four categories for developed land: open space, low, medium, and high intensity. I used the sum of low, medium, and high intensity developed land to calculate the percentage of developed land surrounding each site. The percentage of developed land within the 500m radius of each site ranged from 0.1 – 99% (see Fig S4).

I additionally attempted to acquire management records for each site, including the number and identities of prairies species seeded to initiate restoration, prescribed fire records, and other aspects of management history like the number of times sites were seeded or mowed. However, this information was poorly retained. Since seed mix design, both the richness and density of species, is a strong determinant of prairie restoration outcomes (Glidden et al., 2022; Meissen et al., 2020), I identified species that were likely to have been seeded into each restoration site. To do this, I first compiled a list of all species that were observed during plant community surveys across all sites and a compiled list of all species that were known to have been included in the seed mixes for the plantings surveyed. Seed mix information for the initial seed application was available for 15 out of the 30 sites included in this study. For species not included in seed mixes, I searched Michigan Flora (*Michigan Flora*, 2023) to determine if each species observed was native to Michigan and known to be associated with prairies or prairie-like areas. Species that were either included in the seed mix lists provided or are known to be native to Michigan and associated with prairies and prairie-like areas were considered prairie species.

I also collected data related to management practices such as weeding, mowing, and prescribed burning when available. Most of the sites that had some form of management data had

a record of whether the planting had ever been burned  $(n=26)$ , and this factor was included in preliminary models. However, burning was correlated with the age of the planting and was also a non-significant predictor when included in models for all response variables, thus it was not included in the final set of models.

#### <span id="page-27-0"></span>*Data Analysis*

I performed all analyses in R studio using R version 4.2.3 (R Core Team, 2023). I constructed separate models to assess the roles of site and landscape-level factors for each response variable: plant community composition, prairie and non-prairie species richness, and prairie and non-prairie species cover.

I used a Principal Components Analysis (PCA) to summarize the soil and bioclimatic condition measures (Figs. 2.2, 2.3), as these measures both consisted of several highly correlated factors. The first two axes of the soil attributes PCA explained about 40% of the total variation, hereafter referred to as soil attributes PC1 and soil attributes PC2. Soil attributes PC1 was correlated with clay content, soil pH, and heavy metals like zinc and copper. Soil attributes PC2 was primarily correlated with soil texture and water holding capacity. The value along each PCA axis for each site was extracted and used in both the multivariate and univariate models. Additionally, I used the R package 'dismo' (version 1.3-9; Hijmans et al. 2023) to generate 19 bioclimatic variables (Hijmans et al., 2005) from the PRISM Climate Data (PRISM Climate Group) monthly climate data for each of the planting sites spanning from the year the site was established until the year of survey. The first two loading axes of the bioclimatic attributes PCA explained about 54% of the total variation, hereafter referred to as bioclimatic attributes PC1 and bioclimatic attributes PC2. Bioclimatic attributes PC1 was correlated with precipitation related indicators like drier springs and winters as well as temperature related metrics like diurnal fluctuations. Bioclimatic attributes PC2 was primarily correlated with temperature like warmer annual, spring, and winter temperatures. The value along each PCA axis for each site was extracted and used in both the multivariate and univariate models.

Due to the number of sites in this study  $(n=30)$ , for each of our final models limited to five additive predictor variables: site age, soil attributes PC2, canopy cover, bioclimatic attributes PC2, and the percentage of developed land surrounding each site. Here, I considered site age, soil attributes PC2, canopy cover, and bioclimatic attributes PC2 as site level, or local, factors and the percentage of developed land surround each site as a landscape level factor. I

retained only soil attributes PC2 because it was structured primarily by soil texture and water holding capacity for which I have stronger hypotheses for how these impact plant community establishment than I did for the variables associated with soil attributes PC1. Similarly, I retained only bioclimatic attributes PC2 because it was structured by temperature whereas PC1 was structured more by precipitation, this trend likely being driven by proximity to Lake Michigan and not a reflection of urban site conditions. Of the five predictor variables, only bioclimatic attributes PC2 and the percentage of developed land within a 500m radius buffer of each site were correlated (Pearson's  $R = 0.37$ ), however, the variance inflation factors of the models were <1.5 indicating multicollinearity was low, so all five predictor variables were included in the models. Further, city identity was included in preliminary models, however it was never a significant predictor of the plant community composition, nor prairie and non-prairie species richness or cover, among the prairie planting sites and therefore was not included in the final models.

I used a permutational analysis of variance (PERMANOVA) using the 'adonis2' function of the 'vegan' package (version 2.6-4; Oksanen et al. 2022) to assess community composition and multiple linear regressions using the 'stats' package (R Core Team 2023) to model the roles of local site conditions and landscape context for prairie and non-prairie species richness and cover variables. I examined the residual variance of each model and deemed the normal distribution appropriate for all univariate response variables. Additionally, I visualized the plant community composition data using NMDS ordinations and I utilized the 'envfit' function of the 'vegan' package (version 2.6-4; Oksanen et al. 2022) to fit the site condition and landscape context vectors, as well as vectors of species which may be driving the dissimilarity in plant community composition between sites. Only species that were found to be significant by the 'envfit'' function ( $p < 0.05$ ) were displayed in the ordination figure. I visualized the conditional effects of the significant model factors using the 'ggpredit' function of the 'ggeffects' package (version 1.2.0; Lüdecke 2018) to understand their effect on each response variable.

I tested the effect of spatial autocorrelation among our univariate response variables using a generalized least squares model for each response variable using the 'gls' function from the 'nlme' package (version 3.1-163; Pinheiro & Bate 2023). Models were constructed with and without spatial autocorrelation corrections (exponential, gaussian, linear, rational quadratic, and spherical) and compared using AIC. For all response variables, aside from non-prairie species

richness, the most parsimonious model did not include a spatial autocorrelation correction. For the response variable non-prairie richness, the models with and without the spatial autocorrelation correction were equivalently parsimonious (within 1 AIC point). As there is not a straightforward equivalent test for the multivariate models, I relied on the findings from our linear modeling approach to feel comfortable not including a spatial component to the multivariate models.

#### <span id="page-29-0"></span>**Results**

Variation in plant community composition across the urban prairie plantings was related primarily to site-level factors, such as soil compaction, texture, and water holding capacity  $(F=1.830, R^2=0.060, p=0.009;$  Table A2.1). Additionally, the NMDS ordination (Stress = 0.255, k=2) revealed that the bioclimatic variables related to warmer annual, summer, and winter temperatures (Bioclimatic Attributes PC2), the percentage of developed land cover, canopy openness, and planting site age appeared to form a gradient that restored planting sites tended to fall along (Fig 2.4a). The soil attributes PC axis (Soil Attributes PC2) appeared to form a largely orthogonal axis, relative to the other local and landscape factors plotted within the ordination space (Fig 2.4a). Further, at the species level, it appeared that many of the species that were significantly driving the distribution of restored planting sites within the ordination space were non-prairie, and non-native, species such as *Fallopia convolvulus* (black bindweed), *Chenopodiun album* (white goosefoot), and *Festuca rubra* (red fescue) (Fig 2.4b). Overall, the non-prairie species that may have been driving the distribution of prairie planting sites were aligning with younger, less open canopy sites while prairie species like *Symphyotrichum novaeangliae* (New England aster), *Solidago speciosa* (showy goldenrod)*,* and *Panicum virgatum*  (switchgrass) were aligning with older, more open canopy sites that also exhibited higher levels of surrounding urban land (Fig 2.4b).

Non-prairie species richness and cover were structured primarily by the age of the restoration plantings; there was a decrease in both richness ( $p < 0.05$ ; Table A2.2, Fig 2.3) and cover of non-prairie species with age ( $p < 0.05$ ; Table A2.3, Fig A2.3). Non-prairie species richness was also negatively correlated with soil conditions such as soil compaction, texture, and water holding capacity ( $p < 0.05$ ; Table A2.2, Fig 2.3). Further, there was some evidence that more open canopy conditions reduced non-prairie species richness ( $p = 0.096$ ; Table A2.2, Fig 2.3) while warmer annual, summer, and winter temperatures increased non-prairie species

richness ( $p < 0.05$ ; Table A2.2, Fig 2.3). Although there were no significant predictors of prairie species richness or cover, there was some evidence that sites with warmer annual, summer, and winter temperatures supported lower cover of prairie species ( $p = 0.086$ ; Table A2.3, Fig A2.3). **Discussion**

<span id="page-30-0"></span>Overall, I was able to identify specific factors structuring restoration outcomes in urban contexts and illustrated the importance of local site conditions, not surrounding landscape context, for shaping plant community composition. Site-level factors such as the local climate and the soil conditions were the most significant factors driving variation in the plant community composition among the restored prairie planting sites, while differences in urban land cover in the surrounding landscape explained little variation. However, target, prairie species and nontarget, non-prairie species, did respond to the site-level factors differently.

These findings build on previous work showing how target and non-target plant species tend to respond differently to local scale factors during ecological restoration. In non-urban contexts, soil type and soil resource availability can impact the cover, dominance, and persistence of target and non-target plant species differently, with non-target plant species often able to become dominant across a wider range of soil conditions than target plant species (Daehler, 2003; Gornish & Ambrozio dos Santos, 2016). In contrast, I found that both the richness and cover of target prairie plant species were not correlated with local soil conditions surveyed, but that non-target, non-prairie species did decline in richness as the soil conditions within a planting site became less compacted, had greater water holding capacity, or shifted in soil texture from silty to sandy. The insensitivity of prairie species richness and cover to soil conditions in this study could be due to the species rich nature of prairie plant communities (Risser, 1988) coupled with efficient species sorting along this gradient (e.g., Foster et al. 2011), allowing for maintenance of community-level richness and abundance across the gradient.

Additionally, at the local scale, I found that bioclimatic conditions, such as warmer summers, winters, and annual temperatures led to an increase in the richness of non-target, nonprairie species and – to some extent – a decrease in target prairie species. While local climate conditions have been relatively understudied in non-urban contexts within the field of restoration ecology, it is well known that urbanization can have major impacts on the local climate within urban centers, also referred to as the urban heat island effect (Li et al., 2020; Oke, 1982). I found some evidence for this effect in this study, as there was a correlation ( $r = 0.374$ ,  $p < 0.05$ ) between

the amount of surrounding urban area at a planting site and warmer temperatures. Although this correlation was weak (and did not rise to a problematic level for collinearity in our models), this suggests that at least some variation in temperature was structured by urban landscape context. The finding that warmer summer, winter, and annual temperatures led to an increase in nonprairie species is surprising as prairie species are typically thought to be particularly heat and drought tolerant due to adaptations such as dense root systems to access soil water resources during drought conditions and sun avoiding foliage to reduce heat and light stress in the open canopy conditions of grasslands (Tucker et al., 2011). If the urban heat island effect is detrimental to prairie plant community diversity, restoration practitioners may want to include more heat and drought-adapted prairie species or genotypes in urban restoration plantings expected to be most influenced by the urban heat island phenomena and invest in greater weed control in these plantings to aid in target plant establishment. However, further work is needed to better characterize how local climate within urban settings influences the establishment and assembly of restored plant communities, including effects on individual species which likely vary in their sensitivities.

The surrounding landscape structure was not an important factor shaping urban plant community composition, richness, or cover in this study. Previous work has found that in both urban and non-urban contexts, the surrounding landscape can pose a barrier to plant community assembly by facilitating the movement of invasive species (Skultety & Matthews, 2017), reducing the dispersal of native species due to habitat fragmentation (Overdyck & Clarkson, 2012), and reducing sources of native biodiversity on the landscape through habitat loss (Brudvig & Damschen, 2011; Minor et al., 2009). It seems likely that restoration practices, such as assembling plant communities via seed addition at the planting site, may have overcome the potential barriers to dispersal posed by the surrounding urban land cover within this study. Many of the plant species observed most frequently across prairie planting sites were prairie species, indicating that the seeded prairie species were able to establish and persist once dispersed to the planting site. This lends further support for the ability of restoration practices to overcome potential dispersal limitations created by the urban landscape structure, and points to ecological restoration as a tool to enhance the biodiversity of target, native plant species within urban areas. However, the richness and the cover of non-target, non-prairie species were also not impacted by the surrounding landscape structure either. It could be that the non-target, non-prairie species

were not dispersal limited in these urban landscapes, or these species were recruiting from a soil seed bank and were not reliant on dispersal. More work needs to be done to understand if and when the surrounding landscape structure influences urban restoration projects (e.g. Mitchell et al. 2016).

Restoration practices and management decisions can play a large role in restoration outcomes in non-urban areas (Brudvig & Damschen, 2011; Glidden et al., 2022; Grman et al., 2013), however I found little evidence in support of this within this study. This finding could stem from a lack of management records, such as the identities of sown species and the timing of key management events, like prescribed burns, invasive species removals, and inter-seeding. Such record keeping can open opportunities for future assessment of the role of restoration practices and management decisions with the urban context and research-management partnerships (e.g., Bach & Kleiman 2021).

Overall, I found that many of the types of local site factors that influence plant community composition in non-urban restoration contexts also play a role in shaping plant community composition in urban contexts. However, the ways in which these factors have been modified by urban development may require both the extension of knowledge from non-urban contexts and the development of new frameworks for urban areas. For instance, within this study, sites that had contrasting soil attributes, like increased soil water holding capacity and increased sand content, tended to support similar plant communities (i.e., grouped together within ordination space). More work needs to be done to understand how the modified soils in urban areas influence plant-soil interactions within urban settings (sensu Kotze et al. 2021) to minimize the establishment of non-target plant species within the planting area before beginning ecological restoration (Dighton & Krumins, 2014). Additionally, I found that local climate conditions, such as elevated seasonal and annual temperatures, led to an increase in non-target, non-prairie species richness and a corresponding decrease in target, prairie species. This may indicate a mismatch between the regional climate conditions that target prairie species are adapted to and urban climate conditions, impairing their establishment at a planting site. This suggests that new frameworks need to be developed for urban areas to identify appropriate target species beyond selecting from a regional species pool. Recent work examining trait-environment relationships at the seed mix design stage (Balazs et al., 2020) could provide a relevant framework to build upon in urban systems. Our findings do suggest that more work needs to be

done in both non-urban and urban areas to understand the impact of local climate on plant community development (e.g. Salinitro et al. 2019) and to identify if current ecological restoration techniques are sufficient to address these impacts (Frietsch et al., 2023; Maxwell et al., 2019).

These findings indicate that we can extend generalities of what we know about restoration ecology from non-urban to urban systems, but that specifics of urban restoration efforts should be tailored and may also require new tools. Similar sorts of site level factors, such as the soil and the local climate conditions, are important to take into consideration in both nonurban and urban settings, although the ways in which those conditions have been modified may differ. Further, it seems that tried and tested ecological restoration practices such as sowing the target plant community into the planting site can overcome limitations to dispersal which may be posed by the surrounding landscape context (Grman et al., 2013). However, the impact of local climate conditions in urban areas, potentially stemming from the urban heat island effect, may require new practices to establish resilient plant communities (Frietsch et al., 2023; Maxwell et al., 2019). Overall, urban green spaces hold promise as candidate areas for ecological restoration to increase both the biodiversity of urban areas and the ecosystems services provided by urban green spaces.

## <span id="page-33-0"></span>**Acknowledgements**

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#### FIGURES





**Figure 2.2 a)** NMDS ordination with all site condition and landscape context vectors **b)** NMDS ordination with significant species vectors fit. Stress = 0.255. Prairie planting sites located in Ann Arbor, MI are indicated with red circles, sites located in Grand Rapids, MI are indicated with green triangles, and sites located in Kalamazoo, MI are indicated with blue squares.



**Figure 2.3** Conditional effects of local level factors on non-prairie (a-c) and prairie species (d-f) richness within each of the 30 urban planting sites. **a)** Conditional effect of soil attributes PC2 on non-prairie species richness **b)** conditional effect of site age on non-prairie species richness **c)** Conditional effect of bioclimatic attributes PC2 on non-prairie species richness **d)** Conditional effect of soil attributes PC2 on prairie species richness **e)** Conditional effect of site age on prairie species richness and **f)** Conditional effect of bioclimatic attributes PC2 on prairie species richness. Each black dot represents one of the 30 urban planting sites surveyed. The dark line indicates the regressions of the local scale factor and the non-prairie or prairie species richness, and the grey shaded region represents the 95% confidence interval.


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# APPENDIX

Figure A2.1 PCA to summarize the soil attributes measured at each of the 30 urban prairie planting sites. Each black dot represents one of the 30 urban planting sites surveyed.



**Figure A2.2** PCA to summarize the bioclimatic attributes measured at each of the 30 urban prairie planting sites. Bio1 = Mean annual temperature, bio2 = Mean diurnal range, bio3 = Isothermality, bio4 = Temperature seasonality, bio5 = Max temperature of warmest month, bio6  $=$  Min temperature of coldest month, bio7 = Temperature annual range, bio8 = Mean temperature of the wettest quarter, bio9 = Mean temperature of driest quarter, bio10 = Mean temperature of warmest quarter, bio11 = Mean temperature of coldest quarter, bio12 = Total (annual) precipitation, bio13 = Precipitation of wettest month, bio14 = Precipitation of driest month,  $bio15 = Precipitation seasonality (coefficient of variation), bio16 = Precipitation of wettest$ quarter, bio17 = Precipitation of driest quarter, bio18 = Precipitation of warmest quarter, bio19 = Precipitation of Coldest Quarter. Each black dot represents one of the 30 urban planting sites surveyed.



Figure A2.3 Conditional effects of local level factors on non-prairie (a-c) and prairie species (df) cover within each of the 30 urban planting sites. **a)** Conditional effect of soil attributes PC2 on non-prairie species cover **b)** conditional effect of site age on non-prairie species cover **c)** Conditional effect of bioclimatic attributes PC2 on non-prairie species cover **d)** Conditional effect of soil attributes PC2 on prairie species cover **e)** Conditional effect of site age on prairie species cover and **f)** Conditional effect of bioclimatic attributes PC2 on prairie species cover. Each black dot represents one of the 30 urban planting sites surveyed. The dark line indicates the regressions of the local scale factor and the non-prairie or prairie species cover, and the grey shaded region represents the 95% confidence interval.



**Figure A2.4** Conditional effects of the landscape level factor, the percentage of developed land cover within a 500-meter buffer around each of the planting sites on non-prairie and prairie species richness (a-b) and cover (c-d) within each of the 30 urban planting sites. **a)** Conditional effect of the percentage of developed land cover on non-prairie species richness **b)** Conditional effect of the percentage of developed land cover on prairie species richness **c)** Conditional effect of the percentage of developed land cover on non-prairie species cover and **d)** Conditional effect of the percentage of developed land cover on prairie species cover. Each black dot represents one of the 30 urban planting sites surveyed. The dark line indicates the regressions of the local scale factor and the non-prairie or prairie species richness, and the grey shaded region represents the 95% confidence interval.



**Table A2.1** The output of a PERMANOVA model evaluating how local and landscape-level factors influence plant community composition within 30 urban prairie plantings in southern Michigan. Local level factors include soil attributes PC2, canopy openness, site age, and bioclimatic attributes PC2. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A2.2** The output of a linear regressions model evaluating how local and landscape-level factors influence prairie and non-prairie species richness within 30 urban prairie plantings in southern Michigan. Local level factors include soil attributes PC2, canopy openness, site age, and bioclimatic attributes PC2. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A2.3** The output of a linear regressions model evaluating how local and landscape-level factors influence prairie and non-prairie species cover within 30 urban prairie plantings in southern Michigan. Local level factors include soil attributes PC2, canopy openness, site age, and bioclimatic attributes PC2. The landscape level factor is the percentage of developed land surrounding each planting site.



# CHAPTER THREE: DIFFERENTIAL RESPONSES OF TARGET AND NON-TARGET SPECIES TO LOCAL AND LANDSCAPE-LEVEL FACTORS DROVE PLANT COMMUNITY ASSEMBLY ACROSS AN URBAN CENTER

### **Abstract**

Human land uses threaten biodiversity globally through the alteration of natural ecosystems, but ecological restoration has the potential to halt or reverse these changes. However, restoration outcomes are highly variable: factors such as abiotic site conditions, landscape context, and restoration practices implemented at the restoration site can all lead to mutable restoration outcomes. To refine restoration approaches to be more reliably successful, an understanding of the context dependencies which influence community assembly processes is required. Here, I do so in context of urbanization – a prevalent and growing land-use, influencing biodiversity worldwide. Using a distributed experiment of seeded prairie plots, I tested drivers of variation in target (seeded) and non-target (non-seeded) plant species establishment across an urban center. This approach controls for a major axis of variation, restoration practices, which allows us to better understand the roles of local and landscape-scale factors such as site abiotic conditions and the landscape context for each site. I established 35 small-scale prairie plantings across the Lansing, Michigan (USA) metro area and monitored plant community establishment over two growing seasons. I quantified the importance of site conditions and landscape context for community and individual species responses at each planting site. I found that overall, canopy conditions as well as the amount of urban land cover shaped the plant community at large. Seeded species richness and occurrence was consistently negatively correlated with increasing amount of surrounding urban land cover. Whereas non-seeded species were largely shaped instead by local scale factors like canopy and soil conditions. However, the non-seeded species level results were often idiosyncratic. Parsing target and non-target species responses will aid in the development of restoration practices, such as site preparation methods and seed mixes, to reduce variable outcomes and increase the successful establishment of the target plant community.

#### **Introduction**

Human land uses, including urban expansion, threaten biodiversity globally through the alteration of natural ecosystems (Cardinale et al., 2012). Ecological restoration has the potential to halt or reverse biodiversity loss in human impacted ecosystems, however, restoration

outcomes are variable and often fall short of achieving the same levels of biodiversity and ecosystem functioning as intact ecosystems (Atkinson et al., 2022; Brudvig & Catano, 2021; Rey Benayas et al., 2009). This variation impedes our ability to compare outcomes across restoration efforts, refine approaches to those that are more reliably successful, and inform predictive capabilities. A major challenge to interpreting variable restoration outcomes is the large number of factors that create site specific context dependencies. For example, restoration outcomes may vary based on local site conditions (MacDougall et al., 2008; Stuble et al., 2017; Young et al., 2015), landscape context (Crouzeilles et al., 2016; Woodcock et al., 2010), or the restoration practices implemented (Brudvig & Damschen, 2011; Grman et al., 2013; Guiden et al., 2021). Resolving drivers of variation in restoration outcomes, such as promoting a diverse community dominated by target species, is thus a central goal of restoration science. However, much of the focus of past restoration research attempting to identify consistent drivers of variation among restored areas has not considered how these drivers may differ in urban contexts (Rega-Brodsky et al., 2022), nor how much of our understanding about these drivers will extend to the novel challenges urban ecosystems experience due to urbanization.

Urban land cover is rapidly expanding, increasing by 50% globally over the past 20 years (Potapov et al., 2022). This expansion of urban land cover and associated urbanization processes has resulted in massive changes to urban ecosystems such as the alteration of environmental conditions, like the local climate and soil conditions (Kaye et al., 2006; Pavao-Zuckerman, 2008), which can result in degraded site conditions posing a challenge for plant community establishment within a target restoration site. Additionally, urbanization processes often reconfigure the landscape structure leading to habitat fragmentation and loss (Z. Liu et al., 2016) reducing both the available greenspace and potentially creating barriers to dispersal among urban green spaces. As a result of this degradation and loss of native ecosystems from urban areas due to urbanization there has been a growing interest in supporting and enhancing the biodiversity of urban ecosystems through ecological restoration (Dearborn & Kark, 2010; Nilon et al., 2017).

We can make progress on resolving variable restoration outcomes by understanding the processes structuring arrival to and establishment of target seeded and non-target non-seeded species at a restoration site within urban systems. From work in non-urban systems, we know that limitations to arrival, or dispersal, are common across taxa and systems (Myers & Harms, 2009) and are especially common within the context of ecological restoration (Grman et al.,

2015; Turley et al., 2017), though target and non-target species may respond to these limitations differently. Often, source populations of target species for restoration efforts are rare within the landscape due to human land use driven habitat loss and fragmentation (Haddad et al., 2015; Ibáñez et al., 2014), consequently restoration practitioners explicitly work to overcome arrival limitations for target species through restoration practices such as seed sowing. Non-target nonseeded species tend to be weedy and do not typically face the same dispersal constraints as target seeded species. Non-target species tend to arrive to a restoration site either from the soil seed bank (Overdyck & Clarkson, 2012; Piana et al., 2021) or from the surrounding landscape via seed dispersal mechanisms (White et al., 2009). Within urban systems, dispersal of weedy nontarget species is of special concern as propagules of these non-target species are known to be abundant in the seed rain, soil seed bank, and understory vegetation and pose a significant impediment to restoration efforts (Overdyck & Clarkson, 2012; Wallace et al., 2017).

Likewise, human land uses can leave a lasting impact on a restoration site through impacts to the abiotic site conditions (Foster et al., 2003) which can impede target species establishment once dispersed. The abiotic conditions within a planting site, such as planting year temperature and precipitation (Groves et al., 2020; James et al., 2019), soil conditions (Bassett et al., 2005; Gornish & Ambrozio dos Santos, 2016; Grman et al., 2015), and the light availability (De Queiroz & Maricle, 2019; Mollard & Naeth, 2014), may provide cues for germination postdispersal and promote or impede establishment. However, responses to these site abiotic conditions may vary between target and non-target species within a plant community. For instance, previous work has found increased non-target species richness and cover and decreased target species richness during high precipitation planting years (see Groves et al., 2020). Further, elevated soil temperatures can decrease target species germination (see James et al., 2019). Altered urban environmental conditions such as elevated air temperatures and altered precipitation patterns as a result of the urban heat island effect (Han et al., 2014; Huang et al., 2019) may thus result in an outsized effect of establishment limitations in urban areas. Studies which continue to parse how abiotic site conditions influence the establishment of target and non-target species during ecological restoration efforts are a continued research need within the field of restoration science, especially within urban contexts.

To resolve drivers of variation within the context of ecological restoration, and better understand the context dependencies which may be influencing the assembly processes

structuring both the target and non-target species, experimental approaches are needed (Brudvig et al., 2017). Distributed experiments allow for the control of certain factors such as the restoration practices, while systematically varying others, like local edaphic conditions or landscape context, by replicating the experimental methods across sites (Borer et al., 2014). Distributed experiments have the potential to provide new insights and untangle potential context dependencies for plant community establishment within an ecological restoration framework (e.g., Dickens et al., 2016), especially within urban areas which can be especially variable due to ongoing and historical legacies of human land uses (Aronson et al., 2017). However, disentangling the effects of site-specific establishment limitations from those related to dispersal or the restoration practices remains a persistent challenge (Brudvig et al., 2017).

Using a distributed experimental approach, I aimed to resolve drivers of variation to better understand the context dependencies influencing the assembly processes structuring both the target and non-target plant species across an urban center. This approach controls for a major axis of variation, restoration practices, which allows us to better understand the roles of local and landscape-scale factors such as local edaphic conditions and the surrounding landscape context for each site. I established 35 small-scale prairie plantings across the Lansing, MI, USA metro area and monitored plant community composition, the richness and cover of target and nontarget plant species, and individual species responses over two growing seasons. I then related community and individual species responses to the local abiotic site conditions and the surrounding landscape context of each planting site. Through this experiment, I answered a series of questions: 1) How do local site conditions and landscape context structure the early establishment of prairie plant communities across an urban center? 2) How do target seeded and non-target non-seeded species respond to these local and landscape-scale factors? 3) Are there species-specific responses to these local and landscape-scale factors? I hypothesized that plant community composition and richness would be structured by gradients in local (e.g., soils, microclimate) and landscape (surrounding impervious surface) level attributes. Additionally, I hypothesized that target and non-target species responses would be driven by different suites of factors. For instance, non-target species would be influenced by the surrounding landscape context, whereas target species will not as target species arrival limitation would be alleviated by seed sowing.

### **Methods**

#### *Study Design & Site Selection*

I established 35 small-scale prairie plantings across the greater Lansing, MI (USA) metro area (Fig 3.1). Prairie plant communities have become regionally rare and are a common target for restoration efforts within the Midwest (Lenhart & Smiley 2018), and the restoration of urban grasslands like parks, lawns, and similar urban greenspaces, to native grasslands has been proposed as a potential method to improve landscape connectivity, increase biodiversity, and enhance ecosystem services in urban centers (Klaus, 2013). I selected sites for our small-scale prairie plantings in a mix of public and private greenspaces including private residential yards, church property, nature and community centers, and a school. Prior to being planted into prairie, these greenspaces consisted primarily of turfgrass species, or a mix of turfgrass and bare ground.

I identified potential planting sites through an open call to the surrounding community through email advertising on community listservs. I visited potential sites in May 2021 to determine if the proposed planting area was large enough to accommodate a plot for this study, had mostly open canopy conditions (i.e. was not directly shaded by trees and/or buildings), and was in a low use area to minimize trampling or interference. Two plot sizes were included in this study to maximize the number of participants, 9 m<sup>2</sup> or 4 m<sup>2</sup>, depending on what the landowner could accommodate. I conducted preliminary analyses using plot size as a fixed effect, but since there were no significant differences detected I considered all plots together.

I prepared sites June-December 2021. Site preparation consisted of the removal of the existing plant community from the area by first mowing and then sheet mulching the planting area for one growing season. Sheet mulching is a technique which uses several layers of cardboard to smother the vegetation and block out light, thereby killing the existing plant community. The sheet mulching was removed in December 2021, and I hand-broadcasted the seed mix.

The seed mix consisted of 22 species: six graminoids and 16 forbs supplied by native seed producer Native Connections (Kalamazoo, MI; Table A3.1). The identity of the species included in the seed mix and seeding rate used were based on a standard seed mix (Basic Shortgrass Prairie Seed Mix, Native Connections) for prairie planting efforts in the region, however I modified the seed mix by reducing the number of tall, clump-forming species, like Andropogon gerardi (Big Bluestem) or and subsequently increasing the seeding rate of forbs.

These modifications were made because tall, dense vegetation is typically poorly perceived in urban areas as it reduces visibility through and around plantings, in addition to being perceived as untidy (Gobster et al., 2007; Nassauer & Raskin, 2014).

# *Data Collection – Plant Surveys, Site Conditions, & Landscape Context*

I surveyed the plant community at each site at two scales in July 2022 and 2023: I recorded species identity and cover in a central  $1 \text{ m}^2$  subplot and species presence at the plotlevel. The subplot data provided detailed information about which species were most abundant, and the plot-level data identified which species established at each plot. I recorded the cover of each plant species as the percentage of the subplot occupied by each species present. I surveyed local site conditions known to influence plant germination and establishment during restoration in July 2022 including soil conditions (Gornish & Ambrozio dos Santos, 2016), light availability (De Queiroz & Maricle, 2019; Mollard & Naeth, 2014), climate (Groves et al., 2020), and landscape context (Roy et al., 1999; Schwoertzig et al., 2016). Due to the highly urban nature of many of these plots, I collected soil attribute data likely to be impacted as a result of urbanization such as soil compaction, soil texture, and soil nutrient content (Pavao-Zuckerman, 2008). I measured the depth to soil compaction (depth in cm to 300 PSI), or depth to root growth inhibition, using the Dickey John Soil Compaction Tester in the field. I recorded depth to soil compaction four times at each site, once along each side of the plot, and averaged the values together for each plot. I additionally collected four soil samples from the corners of each plot (diameter= 2 cm, depth= 10 cm). Soil samples were pooled, air dried, and sieved in the lab. I then determined soil texture (the percent of sand, silt, and clay) for these samples using the LaMotte Soil Texture test kit. I also measured soil water holding capacity in the lab for each sample, as the proportional difference between the wet and dry weight of the soil samples using the methods laid out in Brudvig and Damschen (2011). I sent the remaining soil samples from each plot to Brookside Laboratory, Inc. for soil nutrient testing (Soil Test: Standard Soil with Bray I P). I also assessed canopy cover as a proxy for light conditions at each plot using a spherical crown densiometer. I measured canopy cover at each of the plot corners, then averaged these to generate one value for each plot.

To quantify site climatic conditions, I used seasonal and annual temperature and precipitation metrics, which are known to influence prairie plant community establishment (Groves et al., 2020), including mean summer and winter temperature and precipitation using

monthly climate data from PRISM Climate Data (PRISM Climate Group). I quantified local climate conditions separately for each growing season.

I considered the landscape context of each site as the percentage of developed land within a 500m radius, a buffer size which has previously been demonstrated to be most appropriate for understanding the effects of landscape pattern and landscape elements on plant diversity (Z. Z. Li et al., 2018; X. Liu et al., 2022; Purschke et al., 2012), of each site using ArcGIS Pro software and land use/land cover maps produced by the National Land Cover Database Land Cover & Imperviousness for 2019 (Dewitz & U.S.G.S 2021). The National Land Cover Database Landcover & Imperviousness maps include four categories for developed land: open space, low, medium, and high intensity. I used the sum of low, medium, and high intensity developed land to calculate the percentage of developed land surrounding each site. The percentage of developed land within the 500m radius of each site ranged from  $0.1 - 78\%$ .

# *Data Analysis*

I performed all analyses in R studio using R version 4.2.3 (R Core Team, 2023). As I was interested in early establishment dynamics, I conducted separate analyses for each survey year to understand how local and landscape-scale factors influenced plant establishment and assembly dynamics both initially and over the course of two growing seasons. Local factors included the soil conditions, bioclimatic conditions, and canopy cover of each planting site. I considered the percentage of surrounding urban land cover of each site as our landscape-scale factor. I used the same set of additive local and landscape-scale factors in models for each response variable within each year surveyed: plant community composition, seeded and non-seeded species richness, and seeded and non-seeded species cover.

Prior to inclusion in our models, I summarized aspects of the soil conditions with a Principal Components Analysis (PCA), as these measures consisted of several highly correlated factors (Fig. A3.1). The first two loading axes of the soil attributes PCA explained about 44% of the total variation, hereafter referred to as soil attributes PC1 and soil attributes PC2. Soil attributes PC1 was correlated with sand content, soil compaction, soil water holding capacity, and soil nutrients such as potassium (K), manganese (Mn), zinc (Zn), and phosphorus (P). Soil attributes PC2 was primarily correlated with clay and silt content, soil pH, organic matter content, and soil nutrients such as sulfur (S), calcium (Ca), magnesium (Mg), iron (Fe), and copper (Cu). I used PCA axis 1 and 2 values for each site in both the multivariate and univariate

models.

Additionally, I used the R package 'dismo' (version 1.3-9; (Hijmans et al., 2023)) to generate 19 bioclimatic variables (Hijmans et al., 2005) utilizing 800m resolution monthly climate data from the PRISM Climate Data (PRISM Climate Group) for each of the planting sites for each growing season. For the purposes of the local climate data, I considered the first growing season as December 2021, when the planting sites were established, until July 2022 when I surveyed the plant communities for the first time. I considered the second growing season to be from August 2022 until the following July 2023 when I surveyed the plant communities a second time. I summarized these bioclimatic variables, representing aspects of the local climate for each site, prior to inclusion in our models using a PCA (Fig. A3.2, S3.3). During the first growing season, the first two loading axes of the bioclimatic attributes PCA explained about 69% of the total variation, however the second PC axis was heavily influenced by three sites and therefore was not included in either the multivariate or univariate models for the first growing season analyses. The first PC axis, which explained 40.48 % of the total variation, will hereafter be referred to as bioclimatic attributes PC1. Bioclimatic attributes PC1 was correlated with diurnal and annual temperature ranges, annual and winter temperatures, and annual and seasonal precipitation during the first growing season. I used values from the first PCA axis for each site in both the multivariate and univariate models for the first growing season analyses.

During the second growing season, the first two loading axes of the bioclimatic attributes PCA explained about 70% of the total variation, however the second PC axis was also heavily influenced by three sites and therefore was not included in either the multivariate or univariate models for the second growing season analyses. The first PC axis, which explained 43.75 % of the total variation, will hereafter be referred to as bioclimatic attributes PC1. Bioclimatic attributes PC1 was correlated with diurnal and annual temperature ranges and seasonality, annual, summer, and winter temperatures, as well as annual precipitation during the second growing season. I used values from the first PCA axis for each site in both the multivariate and univariate models for the second growing season analyses.

To address our first question examining the effect of local and landscape scale factors on plant community composition, I used a permutational analysis of variance (PERMANOVA) using the 'adonis2' function of the 'vegan' package (version 2.6-4; Oksanen et al. 2022) to develop models for each growing season. Community composition was determined using the

species identity and their cover within the central  $1 \text{ m}^2$  subplot and modeled using the Bray-Curtis dissimilarity metric. Additionally, at the plot level community composition was determined as species identity and modeled using the Jaccard dissimilarity metric. This was determined for both the whole plant community and the target sown plant community as I was especially interested to see how the target sown species may have been influenced by the local and landscape-scale factors. I visualized the plant community composition data using NMDS ordinations and utilized the 'envfit' function of the 'vegan' package (version 2.6-4; Oksanen et al. 2022) to fit the local and landscape-scale factors as vectors.

Additionally, to answer our second question related to understanding how target seeded and non-target non-seeded species respond to these local and landscape-scale factors, I used multiple linear regression models using the 'stats' package (R Core Team 2023) to model the roles of local and landscape-scale factors on target and non-target plant species richness at the subplot and plot level to give a more comprehensive view of the whole planting area and cover at the subplot level where I had recorded species identity and cover to give a more detailed view of abundance. I examined the residual variance of each model and deemed the normal distribution appropriate for all richness and cover response variables at both the plot and subplot level.

To answer our third question related to species-specific responses to these local and landscape-scale factors, I also modeled species level responses of both target and non-target plant species which were observed frequently across plots to the local and landscape variables. Seeded species cover at the subplot level was modeled using multiple linear regressions using the 'lm' function of the 'stats' package (R Core Team 2023) for seeded species that were found in at least 20% of the subplots to assure model convergence. Further, seeded, and non-seeded species presence/absence data at the whole plot level for species that were present in at least 20% of plots but no more than 80% of plots were modeled using multiple general linear models with the binomial distribution and the logit link function using the 'glm' function of the 'stats' package (R Core Team 2023).

Finally, due to the proximity of plots, I tested the effect of spatial autocorrelation among our univariate response variables at both the subplot and plot level using a generalized least squares model for each response variable using the 'gls' function from the 'nlme' package (version 3.1-163; Pinheiro & Bate 2023). I compared models with and without spatial autocorrelation corrections (exponential, gaussian, linear, rational quadratic, and spherical) using

AIC. For all response variables across both growing seasons, the most parsimonious model did not include a spatial autocorrelation correction (within 2 or less AIC points), so I retained only models without spatial autocorrelation correction.

### **Results**

To address our first question related to the impact of local site conditions and landscape context on the early establishment of prairie plant communities, I modeled the effects of local and landscape scale factors on plant community composition at both the subplot and plot level. I found that at the plot level during the first growing season, the plant community was shaped by canopy cover (F = 1.422,  $R^2 = 0.042$ , p = 0.025; Table A3.2). Further during the second growing season, at the plot level, the plant community was shaped by canopy cover ( $F = 2.164$ ,  $R^2 =$ 0.058, p = 0.001; Fig. 3.2; Table A3.3), soil conditions found on soil attributes PC 2 (F = 1.771,  $R<sup>2</sup> = 0.047$ , p = 0.003; Fig. 3.2; Table A3.3) such as increased sand, reduced water holding capacity and soil compaction, and increased levels of soil nutrients such as Potassium (K), Manganese (Mn), Zinc (Zn), Phosphorus (P), and by the amount of urban land cover surrounding the planting sites (F = 2.087,  $R^2 = 0.056$ , p = 0.001; Fig 3.2; Table A3.3). Similarly, at the subplot level during the second growing season, the plant community was also shaped by the same soil conditions (F = 1.641,  $R^2 = 0.047$ , p = 0.012; Table A3.5) and canopy cover (F = 1.456,  $R^2 = 0.041$ ,  $p = 0.039$ ; Table A3.5). There were no other significant predictors of the plant community composition or of the seeded plant community composition across years at either the subplot or the plot level.

To address our second question about the response of the target seeded and non-target non-seeded components of the plant communities I modeled total species richness, seeded species richness, and non-seeded species richness at both the subplot and plot level across growing seasons. I found that at the plot level during the second growing season there was a decrease in both total ( $p = 0.025$ ; Fig. 3.3; Table A3.11) and seeded ( $p = 0.016$ ; Fig. 3.3; Table A3.11) richness with increasing urban land cover surrounding each planting site. There were no other significant predictors of the total, seeded, or non-seeded species richness across years at the subplot or plot level (Tables A3.8-11).

Additionally, I modeled seeded and non-seeded species cover at the subplot level. I observed no correlation between seeded species cover and the local and landscape scale factors across seasons (Tables A3.12, A3.13). However, during the first growing season, I observed

reduced cover of non-seeded species in response to increasing urban land cover surrounding the planting sites ( $p = 0.042$ ; Fig. 3.4g; Table A3.12), local climate conditions such as warmer annual and winter temperatures, reduced variation between summer and winter temperatures, and increased annual and seasonal precipitation ( $p = 0.016$ ; Fig. 3.4e; Table A3.12), and soil conditions ( $p = 0.029$ ; Fig. 3.4a; Table A3.12) such as increased sand, reduced water holding capacity and soil compaction, and increased levels of soil nutrients such as Potassium (K), Manganese (Mn), Zinc (Zn), Phosphorus (P). During the second growing season, I observed reduced cover of non-seeded species in response to increased canopy openness ( $p = 0.007$ ; Fig. 3.4d; Table A3.13) and increased urban land cover surrounding the planting sites ( $p = 0.046$ ; Fig. 3.4h; Table A3.13).

To answer our third question related to species-specific responses, I modeled both the cover at the subplot level and occurrence at the plot level of frequently observed seeded species. I did not find any significant predictors of individual seeded species cover during either the first or second growing season, nor did I observe significant predictors of seeded species occurrence during the first growing season. However, during the second growing season, the occurrence of several seeded species were correlated with the percentage of urban land cover, soil conditions, and local climate conditions. I observed reduced occurrences of *Monarda fistulosa* ( $p = 0.048$ ; Table A3.14), *Verbena stricta* ( $p = 0.024$ ; Table A3.15), and *Penstemon digitalis* ( $p = 0.016$ ; Table A3.16) in response to increased urban land cover surrounding the planting sites. Additionally, I observed fewer occurrences of *V. stricta* (p = 0.044; Table A3.15) in response to soil conditions such as increased sand, reduced water holding capacity and soil compaction, and increased levels of soil nutrients such as Potassium (K), Manganese (Mn), Zinc (Zn), Phosphorus (P), and fewer occurrences of *Ratibida pinnata* (p = 0.024; Table A3.17) in response to local climate conditions such as warmer annual and summer temperatures and increased annual precipitation.

To further address our third question, I also considered species-specific responses for frequently observed non-seeded species. Response to some local factors, such as the soil conditions were mixed for non-seeded species. In response to soil conditions such as increased sand, reduced water holding capacity and soil compaction, and increased levels of soil nutrients such as Potassium (K), Manganese (Mn), Zinc (Zn), Phosphorus (P), I observed reduced cover of *Medicago lupulina* ( $p = 0.015$ ; Table A3.18), but increased cover of *Chenopodium album* ( $p =$ 

0.039; Table A3.19). I also observed increases in the cover of *C. album* in response to additional soil conditions ( $p = 0.010$ ; Table A3.19) such as increased silt, organic matter, and pH as well as soil nutrients like Sulfur (S), Calcium (Ca), Magnesium (Mg), Iron (Fe), Copper (Cu), and Boron (B). Increasingly open canopy conditions led to a consistent decrease in the cover of the nonseeded species *Poa pratensis* (p = 0.007; Table A3.20) and *Acalypha rhomboidea* (p = 0.048; Table A3.21). In response to local climate conditions such as warmer annual and winter temperatures, reduced variation between summer and winter temperatures, and increased annual and seasonal precipitation I observed an increase in the cover of the non-seeded *Plantago lanceolata* (p = 0.013; Table A3.22) while increasing urban land cover surrounding the planting sites led to an increase in the cover of the non-seeded *Solanum nigrum* (p < 0.001; Table A3.23).

During the second growing season, decreasing canopy cover again led to a decrease in the cover of a non-seeded species, *Poa pratensis* (p = 0.032; Table A3.24). Local climate conditions such as warmer annual and summer temperatures and increased annual precipitation led to a decrease in the observed cover of the non-seeded *Taraxacum officinale* (p = 0.047; Table A3.25). While soil conditions such as increased silt, organic matter, and pH as well as soil nutrients like Sulfur (S), Calcium (Ca), Magnesium (Mg), Iron (Fe), Copper (Cu), and Boron (B) led to an increase in the observed cover of the non-seeded species *Solidago canadensis* (p = 0.034; Table A3.26).

Non-seeded species occurrences during the first growing season were primarily driven by soil conditions, local climate conditions, and canopy conditions. In response to soil conditions such as increased silt, organic matter, and pH as well as soil nutrients like Sulfur (S), Calcium (Ca), Magnesium (Mg), Iron (Fe), Copper (Cu), and Boron (B), I observed fewer occurrences of *P. lanceolata* ( $p = 0.050$ ; Table A3.27) but increased occurrences of *S. canadensis* ( $p = 0.049$ ; Table A3.28). I observed fewer occurrences of *Digitaria sanguinalis* ( $p = 0.045$ ; Table A3.29) and *Rumex obtusifolius* ( $p = 0.029$ ; Table A3.30) in response to local climate conditions such as warmer annual and winter temperatures, reduced variation between summer and winter temperatures, and increased annual and seasonal precipitation. Additionally, decreased canopy cover led to a decrease in the occurrence of *Glechoma hederacea* ( $p = 0.037$ ; Table A3.31).

During the second growing season, non-seeded species occurrences had more consistent responses to local scale factors such as the soil and canopy conditions, but had inconsistent response to the landscape scale factors, surrounding urban land cover. I observed more

occurrences of the non-seeded *T. officinale*  $(p = 0.025$ ; Table A3.32), *S. canadensis*  $(p = 0.049$ ; Table A3.33)*,* and *Symphyotrichum pilosum* (p = 0.013; Table A3.34) in response to soil conditions such increased silt, organic matter, and pH as well as soil nutrients like Sulfur (S), Calcium (Ca), Magnesium (Mg), Iron (Fe), Copper (Cu), and Boron (B). In contrast, I observed fewer occurrences of the non-seeded species *O. stricta* (p = 0.020; Table A3.35)*, G. hederacea*   $(p = 0.014;$  Table A3.36)*, and Cerastium fontanum*  $(p = 0.028;$  Table A3.37) in response to an increase in canopy openness. However, in response to increasing amounts of urban land cover surrounding the planting sites, I observed fewer occurrences of *Elymus repens* (p = 0.032; Table A3.38) and *G. hederacea* (p = 0.049; Table A3.36)*,* but more occurrences of *Trifolium repens* (p  $= 0.041$ ; Table A3.39).

# **Discussion**

Resolving drivers of variation that limit target plant community establishment within urban contexts is an important step towards improving restoration outcomes and predictability. By using a common experimental design across a distributed network of urban restoration plantings, I found that local and landscape level factors such as the soil, local climate, and light conditions as well as the amount of surrounding urban land cover influenced plant community composition. However, I did not find the same pattern for the seeded plant community composition. The community level patterns were driven by the different responses of seeded and non-seeded species richness and cover to these factors.

I found some support for our hypothesis that landscape context would influence the establishing prairie communities in this study. Increasing amounts of urban land cover surrounding the planting sites led to a decrease in total species richness ( $p = 0.025$ ; Fig 3.3; Table A3.11) and this was driven by the decline in seeded species richness ( $p = 0.016$ ; Fig 3.3; Table A3.11). At the individual species level, I also observed this pattern for several seeded species: occurrences of *M. fistulosa, V. stricta,* and *P. digitalis*, were negatively correlated with the amount of surrounding urban land cover (Table 3.1). Differential emergence and establishment of seeded species in response to the amount of urban land cover could be tied to the impact of impervious surfaces on the local climate. This so-called "urban heat island effect" and can lead to local climate conditions, such as elevated air temperatures, that are not suitable for certain plant species (Czaja et al., 2020; Y. Li et al., 2020; Oke, 1982). In this study, I found some evidence for this as there was a positive correlation between the amount of surrounding

urban land cover at a planting site and the local climate conditions during the first ( $r = 0.449$ ,  $p <$ 0.05) and second ( $r = 0.446$ ,  $p < 0.05$ ) growing seasons. Although this correlation was weak and did not rise to a problematic level for collinearity in our models (VIFs < 2), it does suggest that at least some variation in temperature, and perhaps additional local climate conditions, was structured by urban landscape context. Urban land cover did not drive changes in the non-seeded species richness across sites; however, it did drive reductions in the cover of non-seeded species across both growing seasons (Fig. 4g, 4h). The impact of the amount of surrounding urban land cover on the cover, but not richness, of the non-seeded plant species could be due to a lack of dispersal limitation for a core set of species (Overdyck & Clarkson, 2012; Wallace et al., 2017). Additionally, as stated above, more highly urbanized areas may have more stressful environmental conditions for plants, reducing their growth and therefore cover.

Seeded species cover and richness were largely insensitive to the local level factors measured. In fact, many of the species that reliably established (> 60% of planting sites; Table 3.1), like *R. hirta, C. lanceolata, S. rigida,* and *E. purpurea*, were not correlated with any of the local or landscape level factors measured and thus may be ideal candidates for broad use in future urban restoration efforts. However, some of the seeded species occurring less frequently (~35-60% of the planting sites; Table 3.1) that were correlated with soil conditions (i.e., *V. stricta*) such as increased sand, reduced water holding capacity and soil compaction, and increased levels of soil nutrients such as Potassium (K), Manganese (Mn), Zinc (Zn), Phosphorus (P), local climate conditions (i.e., *R. pinnata*), and the surrounding landscape context (i.e., *M. fistulosa*) should be used in a more targeted approach to match species with suitable site conditions. Species that rarely established  $(-5-35\%$  of planting sites; Table 3.1) but did not correlate with any of the local or landscape level factors measured (i.e., *Solidago nemoralis*) require future study to better understand which site conditions and landscape contexts favor their establishment in future urban restoration efforts. I also found that several seeded species never emerged (i.e., *Aster azureus*) and are thus not recommended for inclusion in future urban restoration efforts at this time.

In contrast, the occurrence and cover of non-seeded species was commonly related to local scale site conditions, such as the soil, canopy cover, and local climate. Even though many of the non-seeded species observed are considered common weeds of lawns, roadsides, and other urban land use types, their responses to the local site conditions were often idiosyncratic across

species. For instance, soil conditions such as increased silt, organic matter, and pH as well as soil nutrients like Sulfur (S), Calcium (Ca), Magnesium (Mg), Iron (Fe), Copper (Cu), and Boron (B) predominantly led to increased cover and occurrences of several individual non-seeded species, such as *S. canadensis* and *T. officinale*, during both growing seasons. This could be because soil with more silt, clay, and organic matter retains soil moisture, leading to better conditions for germination and establishment. Conversely, soil conditions such as increased sand, reduced water holding capacity and soil compaction, and increased levels of soil nutrients such as Potassium (K), Manganese (Mn), Zinc (Zn), Phosphorus (P) sometimes led to increased cover of non-seeded species, like *C. album*, but also led to a decrease in the overall cover of non-seeded species as a group, especially during the first growing season. Sandier soils are typically less fertile and less likely to develop persistent soil seed banks (Leck, 2012). The increase in the cover of non-seeded species in response to these sandier soil conditions during the first growing season, and no response to these conditions during the second growing season, could be due a response of non-seeded species from soil seed bank in sites with more fertile soils.

I also found that the cover of non-seeded species ( $p = 0.007$ ; Fig. 3.4d; Table A3.13), as well as the cover and occurrence of several individual non-seeded species, like *G. hederacea*, increased when plots experienced more canopy cover. This reduction in cover and occurrence may be the result of non-seeded species being outcompeted by seeded species in more open canopy conditions, as prairie plant species are well adapted to high-light conditions (Tucker et al., 2011). Or that the reduction in cover and occurrence of non-seeded species might be due to the response of shade-adapted non-seeded species. It is notable, however, that neither prairie species richness nor cover declined with increasing canopy cover. Despite this, shadier sites may not be ideal for prairie restoration efforts as they may support weedier plant communities.

Sites which experienced wetter and warmer conditions at the time of seeding and early in the first growing season supported higher cover of non-seeded species, like *P. lanceolata* (p = 0.016; Fig. 3.4e; Table A3.12). These findings build on past work from non-urban prairie restorations, which showed that planting years experiencing greater rainfall can support greater non-seeded species richness and abundance (e.g. Groves & Brudvig, 2019). However, during the second growing season of this study, I found some evidence that sites experiencing cooler annual and summer temperatures supported higher levels of non-seeded species cover ( $p = 0.052$ ; Fig. 3.4f; Table A3.13). The reason for this is unclear, however cooler annual and summer

temperatures could support soil moisture retention which in turn could favor germination of nonseeded species from the soil seed bank (Kathiresan & Gualbert, 2016). Or, wetter and warmer conditions during the previous growing season could have led to increased seed production on non-seeded species, contributing to the available weed soil seed bank for the following growing season (Kathiresan & Gualbert, 2016).

This study indicates that local site conditions and landscape context play a role in the early establishment of prairie plant communities across an urban center. I found that richness and cover, as well as the occurrence, of many of the target seeded species were relatively insensitive to the gradients in the local site conditions measured, indicating that prairie plant communities may indeed be good candidates for urban restoration efforts. However, I also found that the establishment of plant communities dominated by the target plant community may require careful consideration of the local site conditions to control the non-seeded plant community. For instance, sites which feature more open canopy conditions and less surrounding urban land cover, and planting years which are drier, and cooler may favor lower cover and occurrence of non-seeded species, while promoting seeded species establishment. Overall, this study indicates that ecological restoration of urban greenspaces is feasible, and that variation in outcomes can be interpreted through the lens of differential target and non-target species responses.

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# FIGURES



**Figure 3.1** Map of the 35 urban prairie plantings across the Lansing, MI (USA) metro area. Black markers indicate site locations.

**Figure 3.2** NMDS ordination with all site condition and landscape context vectors for plot level plant community data in 2023. Stress = 0.23. Prairie planting sites are indicated with black dots.







**Figure 3.4** Conditional effects of local and landscape level factors on non-seeded species cover within each of the 35 planting sites: a) soil attributes PC2 during the first growing season b) soil attributes PC2 during the second growing season c) canopy openness during the first growing season d) canopy openness during the second growing season e) bioclimatic attributes PC1 during the first growing season f) bioclimatic attributes PC1 during the second growing season g) surrounding urban land cover during the first growing season h) surrounding urban land cover during the second growing season. Each black dot represents one of the 35 planting sites. The dark line indicates the regressions of the local scale factor and the non-prairie or prairie species



# TABLES

**Table 3.1** Frequency of observation for seeded species recorded during 2023 plot surveys and interaction with predictor variables if applicable. Seeded species that were not observed include: *Sporobolus heterolepis* (Prairie Dropseed), *Aster azureus* (Sky Blue Aster), *Baptisia tinctoria* (Small Yellow Wild Indigo), and *Potentilla arguta* (Prairie Cinquefoil).



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## APPENDIX





**Figure A3.2** PCA to summarize the bioclimatic attributes measured at each of the 35 prairie planting sites during the first growing season. Bio1 = Mean annual temperature, bio2 = Mean diurnal range, bio3 = Isothermality, bio4 = Temperature seasonality, bio5 = Max temperature of warmest month, bio6 = Min temperature of coldest month, bio7 = Temperature annual range,  $bio8 = Mean temperature of the wettest quarter, bio9 = Mean temperature of the water, bio10$  $=$  Mean temperature of warmest quarter, bio11 = Mean temperature of coldest quarter, bio12 = Total (annual) precipitation,  $bi013$  = Precipitation of wettest month,  $bi014$  = Precipitation of driest month, bio15 = Precipitation seasonality (coefficient of variation), bio16 = Precipitation of wettest quarter, bio17 = Precipitation of driest quarter, bio18 = Precipitation of warmest quarter, bio19 = Precipitation of Coldest Quarter. Each black dot represents one of the 35 planting sites included in this study.



**Figure A3.3** PCA to summarize the bioclimatic attributes measured at each of the 35 prairie planting sites during the second growing season. Bio1 = Mean annual temperature, bio2 = Mean diurnal range, bio3 = Isothermality, bio4 = Temperature seasonality, bio5 = Max temperature of warmest month, bio6 = Min temperature of coldest month, bio7 = Temperature annual range,  $bio8 = Mean temperature of the wettest quarter, bio9 = Mean temperature of the water, bio10$  $=$  Mean temperature of warmest quarter, bio11 = Mean temperature of coldest quarter, bio12 = Total (annual) precipitation,  $bi013$  = Precipitation of wettest month,  $bi014$  = Precipitation of driest month, bio15 = Precipitation seasonality (coefficient of variation), bio16 = Precipitation of wettest quarter, bio17 = Precipitation of driest quarter, bio18 = Precipitation of warmest quarter, bio19 = Precipitation of Coldest Quarter. Each black dot represents one of the 35 planting sites included in this study.



**Table A3.1** List of seeded species.



**Table A3.2** The output of a PERMANOVA model evaluating how local and landscape-level factors influence plant community composition at the plot level during the first growing season within 35 prairie planting sites across the Lansing, MI metro area using the Jaccard dissimilarity metric. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.3** The output of a PERMANOVA model evaluating how local and landscape-level factors influence plant community composition at the plot level during the second growing season within 35 prairie planting sites across the Lansing, MI metro area using the Jaccard dissimilarity metric. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.4** The output of a PERMANOVA model evaluating how local and landscape-level factors influence plant community composition at the subplot level during the first growing season within 35 prairie planting sites across the Lansing, MI metro area using the Bray-Curtis dissimilarity metric. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.5** The output of a PERMANOVA model evaluating how local and landscape-level factors influence plant community composition at the subplot level during the second growing season within 35 prairie planting sites across the Lansing, MI metro area using the Bray-Curtis dissimilarity metric. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.6** The output of a PERMANOVA model evaluating how local and landscape-level factors influence the seeded plant community composition at the subplot level during the first growing season within 35 prairie planting sites across the Lansing, MI metro area using the Bray-Curtis dissimilarity metric. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.7** The output of a PERMANOVA model evaluating how local and landscape-level factors influence the seeded plant community composition at the subplot level during the second growing season within 35 prairie planting sites across the Lansing, MI metro area using the Bray-Curtis dissimilarity metric. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.8** The output of linear regression models evaluating how local and landscape-level factors influence the total species richness, seeded species richness, and non-seeded species richness at the subplot level during the first growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.9** The output of linear regression models evaluating how local and landscape-level factors influence total richness, seeded species richness, and non-seeded species richness at the subplot level during the second growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.10** The output of a linear regressions model evaluating how local and landscape-level factors influence the total species richness, seeded species richness, and non-seeded species richness at the plot level during the first growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.11** The output of a linear regressions model evaluating how local and landscape-level factors influence the total species richness, seeded species richness, and non-seeded species richness at the plot level during the second growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.12** The output of linear regression models evaluating how local and landscape-level factors influence seeded and non-seeded species cover at the subplot level during the first growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.13** The output of linear regression models evaluating how local and landscape-level factors influence seeded and non-seeded species cover at the subplot level during the second growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.14** The output of a linear regression model using the binomial distribution and the logit link function evaluating how local and landscape-level factors influence the presence of a seeded species, *Monarda fistulosa*, at the plot level during the second growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.15** The output of a linear regression model using the binomial distribution and the logit link function evaluating how local and landscape-level factors influence the presence of a seeded species, *Verbena stricta*, at the plot level during the second growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.16** The output of a linear regression model using the binomial distribution and the logit link function evaluating how local and landscape-level factors influence the presence of a seeded species, *Penstemon digitalis*, at the plot level during the second growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.17** The output of a linear regression model using the binomial distribution and the logit link function evaluating how local and landscape-level factors influence the presence of a seeded species, *Ratibida pinnata*, at the plot level during the second growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.18** The output of a linear regression model evaluating how local and landscape-level factors influence the cover of a non-seeded species, *Medicago lupulina*, at the subplot level during the first growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.19** The output of a linear regression model evaluating how local and landscape-level factors influence the cover of a non-seeded species, *Chenopodium album*, at the subplot level during the first growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.20** The output of a linear regression model evaluating how local and landscape-level factors influence the cover of a non-seeded species, *Poa pratensis*, at the subplot level during the first growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.21** The output of a linear regression model evaluating how local and landscape-level factors influence the cover of a non-seeded species, *Acalypha rhomboidea*, at the subplot level during the first growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.22** The output of a linear regression model evaluating how local and landscape-level factors influence the cover of a non-seeded species, *Plantago lanceolata*, at the subplot level during the first growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.23** The output of a linear regression model evaluating how local and landscape-level factors influence the cover of a non-seeded species, *Solanum nigrum*, at the subplot level during the first growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.24** The output of a linear regression model evaluating how local and landscape-level factors influence the cover of a frequently observed non-seeded species, *Poa pratensis*, at the subplot level during the second growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.25** The output of a linear regression model evaluating how local and landscape-level factors influence the cover of a frequently observed non-seeded species, *Taraxacum officinale*, at the subplot level during the second growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.26** The output of a linear regression model evaluating how local and landscape-level factors influence the cover of a frequently observed non-seeded species, *Solidago canadensis*, at the subplot level during the second growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.27** The output of a linear regression model using the binomial distribution and the logit link function evaluating how local and landscape-level factors influence the presence of a nonseeded species, *Plantago lanceolata*, at the plot level during the first growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.28** The output of a linear regression model using the binomial distribution and the logit link function evaluating how local and landscape-level factors influence the presence of a nonseeded species, *Solidago canadensis*, at the plot level during the first growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.29** The output of a linear regression model using the binomial distribution and the logit link function evaluating how local and landscape-level factors influence the presence of a nonseeded species, *Digitaria sanguinalis*, at the plot level during the first growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.30** The output of a linear regression model using the binomial distribution and the logit link function evaluating how local and landscape-level factors influence the presence of a nonseeded species, *Rumex obtusifolius*, at the plot level during the first growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.31** The output of a linear regression model using the binomial distribution and the logit link function evaluating how local and landscape-level factors influence the presence of a nonseeded species, *Glechoma hederacea*, at the plot level during the first growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.32** The output of a linear regression model using the binomial distribution and the logit link function evaluating how local and landscape-level factors influence the presence of a seeded species, *Taraxacum officinale*, at the plot level during the second growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.


**Table A3.33** The output of a linear regression model using the binomial distribution and the logit link function evaluating how local and landscape-level factors influence the presence of a seeded species, *Solidago canadensis*, at the plot level during the second growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.34** The output of a linear regression model using the binomial distribution and the logit link function evaluating how local and landscape-level factors influence the presence of a seeded species, *Symphyotrichum pilosum*, at the plot level during the second growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.35** The output of a linear regression model using the binomial distribution and the logit link function evaluating how local and landscape-level factors influence the presence of a seeded species, *Oxalis stricta*, at the plot level during the second growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.36** The output of a linear regression model using the binomial distribution and the logit link function evaluating how local and landscape-level factors influence the presence of a seeded species, *Glechoma hederacea*, at the plot level during the second growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.37** The output of a linear regression model using the binomial distribution and the logit link function evaluating how local and landscape-level factors influence the presence of a seeded species, *Cerastium fontanum*, at the plot level during the second growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.38** The output of a linear regression model using the binomial distribution and the logit link function evaluating how local and landscape-level factors influence the presence of a seeded species, *Elymus repens*, at the plot level during the second growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



**Table A3.39** The output of a linear regression model using the binomial distribution and the logit link function evaluating how local and landscape-level factors influence the presence of a seeded species, *Trifolium repens*, at the plot level during the second growing season within 35 prairie planting sites across the Lansing, MI metro area. Local level factors include soil attributes PC1, soil attributes PC2, canopy openness, and bioclimatic attributes PC1. The landscape level factor is the percentage of developed land surrounding each planting site.



## CHAPTER FOUR: CONSEQUENCES OF ROAD SALT DEPOSITION ON NATIVE PLANT COMMUNITY ASSEMBLY

## **Abstract**

Road networks are extensive globally. Furthermore, the environmental conditions along them are often hot, dry, and polluted which can result in an altered ecology for many species, including native plant communities. This is especially so in regions where de-icing salts are applied seasonally for winter road management. To ameliorate the detrimental effects of road pollution, restore connectivity between green spaces in urban areas, and enhance ecosystem services there has been increasing interest in roadside native plant community restoration. However, we do not currently know how specific stressors associated with roadside environments, such as salt deposition, influence establishing plant communities during restoration. Moreover, we currently lack understanding of how different species and genotypes within species vary in their tolerance to roadside soil conditions, limiting the capacity to conduct restoration in the face of these conditions. Here, I experimentally investigated the effects of winter road salt application on the emergence and establishment of prairie plant communities, which are a common focus of roadside restoration efforts throughout the U.S. Midwest and Great Plains. Additionally, I tested the effects of road salt concentration on both Midwest and coastally sourced genotypes of some seeded species, which I hypothesized to vary in tolerance due to adaptation to natural salt deposition for the coastal source. There were clear effects of salt deposition for plant community establishment and on the seeded prairie plant species. Although prairie plants were able to establish at all levels of salt deposition, even low levels of salt deposition had negative impacts which magnified at intermediate to high levels of salt deposition. I did not find any evidence that coastal seed sourcing mitigated these effects, and, in fact, there was at least some evidence that coastal sources performed worse. Local seed sources are thus likely sufficient, and in some cases may be better suited due to local adaptation to other environmental conditions not tested for in this study, for roadside restoration. Species varied in their responses to salt, but even for the best establishing species, most showed clear detrimental effects of salt deposition. This study suggests that prairie plant communities, and prairie species which established reliably across salt treatments, are good candidates for roadside restoration. Due to its ubiquitous negative effects, efforts to reduce salt deposition on roadside vegetation will lead to roadside prairie restoration that is most effective.

### **Introduction**

Road networks are extensive globally. For instance, the United States has a road network totaling over six million km (U.S. Department of Transportation Bureau of Transportation Statistics, 2022), and in most places in the conterminous U.S. the distance to the next nearest road is less than 35 km (U.S. Geological Survey, 2005; Watts et al., 2007). The environmental impacts of road networks predominately stem from pollution including exhaust from vehicle emissions (e.g.  $NO<sub>x</sub>$ , CO, and particulates), altered microclimate conditions, and poor soil conditions resulting from compacted and imported soil and gravel ("fill" material) which often contains high levels of herbicide, metals, and de-icing salts from winter road management (Forman, 2003; Haan et al., 2012). Urbanized areas can experience compounding effects from roads as there is more overlap in the "road-effect zone" (e.g. 1 km from road; Phillips et al., 2021), due to the higher proportion of roads and impervious surfaces (Findlay & Kelly, 2011). This dense road network presents a challenging environment for many species (Coffin, 2007), including native plant communities, and understanding these effects and ways to mitigate them are key knowledge gaps.

There has been increasing interest in native plant community restoration along roadsides to ameliorate the detrimental effects of road pollution, restore connectivity between green spaces in urban areas, and enhance ecosystem services. Several studies have examined the effect of roadside conditions on certain functional groups like woody species (e.g. Bryson & Barker, 2002; Equiza et al., 2017). Additional studies have examined roadside restoration outcomes for specific ecosystem services such as erosion control (e.g. Bochet et al., 2010; Tormo et al., 2007), but open questions remain about the ability to restore native plant communities along roadsides given the altered soil conditions observed. For instance, the seasonal reapplication of de-icing salts has increased in recent decades and now exceeds 20 million metric tons annually in the U.S. (Hintz et al., 2022). De-icing salts can be moved from immediately adjacent to roadsides to further into the surrounding area via snow ploughs, splash and spray from moving vehicles, wind, and snowmelt runoff (Lax & Peterson, 2009). Much of that salt persists in the soil for years (Lax & Peterson, 2009; Lundmark & Olofsson, 2007), which presents a challenge to roadside native plant community restoration efforts.

Although previous work has indicated that de-icing salts can suppress native vegetation (Thompson & Rutter, 1986), we currently do not understand how de-icing salts influence the

early establishment dynamics of native plant communities undergoing restoration. In general, salt-impacted soils can hamper germination by restricting water uptake which is required to initiate the germination process (Ryan et al., 1975). Further, high levels of salt in the soil can also cause water stress and salt accumulation in the leaves of establishing plants resulting in salt toxicity (Ryan et al., 1975). The potentially negative impacts of de-icing salt deposition on the early establishment dynamics of native plant species is especially problematic, as many restoration efforts rely on seed addition to establish a target plant community, due to its low cost and ease of dispersing seeds (Barak et al., 2021). Moreover, little is known about how the effects of de-icing salt deposition along roads may differ among or within species of native plant communities (but see Blanchard et al., 2023), in spite of likely variation among species. For instance, C4 grasses, a major functional group in prairie plant communities, have remarkable abilities to tolerate hot, dry, and even salty conditions and, thus, may be suited to roadside conditions (Dudley et al., 2014; Pardo & VanBuren, 2021). Other species or functional groups may lack adaptations necessary to tolerate salty conditions, especially for native plant communities that do not experience natural exposure to salt deposition, such as prairie plant communities in the Midwest and Great Plains.

Alternatively, local adaptations to salty conditions may exist within species, especially when a species' distribution includes coastal regions which could help promote restoration success in the face of winter road salt deposition. Populations found in coastal regions may contain genotypes which are more tolerant of salt due to historic exposure from marine sources (Busoms et al., 2023; Itoh, 2021; Lowry et al., 2008), and thus, may be naturally adapted to roadside conditions. However, distance to the ocean and other factors such as soil type have been found to drive the degree and type of salt tolerance adaptations. This suggests the possibility that sourcing plants from coastal regions, even if not local to a project site, might benefit roadside restoration efforts. However, the predominant paradigm within the field of seed-based restoration is in line with recent changes to public policy which states that local, or geographically near (Hereford, 2009; Whitlock, 2015), seed sources should be utilized whenever possible to achieve the best restoration outcomes as local seed sources are more likely to be locally adapted to the planting site than non-local (Gustafson et al., 2005; McKay et al., 2005; Riley & Wilkinson, 2007). However, this paradigm does not take into consideration the novel conditions present in urban and roadside restoration efforts, many of which likely do not have a "local" populations of

target species to source from. With this, urban and roadside restoration success may require novel methods such as sourcing seed to incorporate salt tolerant species or genotypes within a seed mix to create a potentially more resilient plant community.

To understand the consequences of salt deposition on roadside plant communities, I experimentally tested winter road salt application on prairie plant community emergence and establishment. I applied five concentration levels of road salt to simulate the differences in road salt application with increasing distance from the roadside. I then investigated a possible management tool, seed sourcing, by testing the effects of road salt concentration on both Midwest and coastally sourced seeds of 11 species, which may be adapted to higher salt concentrations due to increased salt deposition in coastal regions of prairie species' native ranges. I addressed the following questions: How does increased road salt deposition structure the initial establishment of prairie plant communities from seed? Do populations sourced from coastal areas establish better when exposed to road salt deposition than populations sourced from the Midwest? Are there species-specific responses to salt deposition? I hypothesized that salt deposition would alter community composition, reduce rates of prairie plant establishment, and the diversity and cover of prairie plant species. I also hypothesized that these effects would be at least partly mitigated by the inclusion of coastal genotypes, although there would be variation among species, with groups including C4 grasses showing reduced effects of salt deposition on their establishment.

## **Methods**

## *Study Design*

I conducted this study at the Lux Arbor Reserve Delton, Michigan (USA), within an area supporting an herbaceous old field prior to the start of the study. This study consisted of a crossed manipulation between salt addition (5 levels;  $0$ ,  $25$ ,  $50$ ,  $75$ ,  $100g$  NaCl/m<sup>2</sup>) and seed source (2 levels; coastal genotypes included for a subset of species vs. Midwest genotypes only). I prepared the old field from June-August 2021 via repeated Glyphosate herbicide treatment and mowing to remove the existing plant community. I laid 120 (12 plots/treatment), 4  $m<sup>2</sup>$  plots separated by a 1-meter buffer and seeded each plot in December 2021 with a prairie seed mix consisting of 25 species: 7 grasses/sedges and 18 species of forbs (Table A1). Each plot was seeded with the same 25 species, but half of the plots within each salt treatment were seeded with species entirely sourced from the Midwest (seed provided by Native Connections located in

Kalamazoo, MI) and half of the plots within each salt treatment included seed sourced from a coastal native plant nursery (Pinelands Nursery located in Columbus, NJ) for two graminoid species and nine forb species, with the remainder of the seed mix consisting of the Midwest sourced seed for remaining grasses and forbs (Table A4.1). All combinations of salt and source treatments were randomly applied across the plot array.

I applied the salt treatment during the winter beginning in December 2021 and again beginning in December 2022. I applied the salt treatment every three weeks for a total of four salt applications per winter, to simulate winter road salt deposition.

## *Data Collection – Plant Surveys & Soil Electrical Conductivity Testing*

I monitored the plant community composition over two growing seasons in each plot in July 2022 and July 2023. I recorded the cover of each plant species as the percentage of the plot occupied by each species present. Additionally, I monitored seeded species establishment through counts of seeded species during the first growing season in July 2022.

To understand the consequences of the salt treatments on plots, and to confirm their effects for soil salinity, I monitored soil electrical conductivity levels as a proxy for salt content (Corwin & Yemoto, 2020). I collected soil cores at each of the corners of the plots using a soil corer (diameter= 2cm, depth= 20cm) in June 2022, August 2022, April 2023, June 2023, and August 2023. The soil cores were pooled by plot then air dried in the lab and sieved prior to testing. I saturated soil samples from each plot and from each sampling round with deionized water and recorded the electrical conductivity (mS/cm) of the soil paste sample using an electrical conductivity meter and corresponding probe (Hanna Instruments HI9813-61/ HI1285- 61).

#### *Data Analysis*

I performed all analyses in R studio using R version 4.2.3 (R Core Team, 2023). I constructed separate models to assess the roles of seed source, salt addition level, and the interaction of those factors for each response variable: plant community composition, cover of seeded and non-seeded species, richness of seeded species, and counts of seeded species.

To assess the plant community composition, I used plant species cover within each plot for both survey years and a permutational analysis of variance (PERMANOVA) using the 'adonis2' function of the 'vegan' package (version 2.6-4; Oksanen et al. 2022) with the Bray-Curtis dissimilarity metric. Seed source, salt addition level, and the interaction of those factors

were included as fixed effects. Additionally, I visualized the plant community composition data using non-metric multidimensional scaling (NMDS) ordinations. I examined the effects of seed source, salt treatment, and the interaction of these fixed effects on seeded species cover, nonseeded species cover, and seeded species richness through multiple linear regression models using the 'lm' function of the 'stats' package (R Core Team 2023).

To assess rates of establishment for the seeded species, I took two approaches. I first summed counts of individuals across all seeded species observed in a plot together due to the scarcity of many seeded species during the first growing season. I used a linear regression model using the 'lm' function of the 'stats' package (R Core Team 2023) to model the effect of seed source, salt addition level, and the interaction between these fixed effects. Further, for seeded species that were observed in one third or more of all plots and of those plots there was representation in both seed sourcing treatments (if applicable), I developed individual models using the 'glm' function of the 'stats' package (R Core Team 2023), the 'glm.nb' function of the 'MASS' package (version 7.3-58.2; (Venables & Ripley, 2002), and the 'zeroinlf' function of the 'pscl' package (version 1.5.5.1; Zeileis et al., 2008). To aid model selection, the conditional means and variances for each species were calculated and data for each species were checked for potential issues with zero inflation. I selected final models for each species through a check of AIC comparison using the 'AIC' function of the 'stats' package (R Core Team 2023).

To ensure that the winter salt deposition treatments were effective, I modeled soil electrical conductivity within and across years by treatment to better understand how repeated annual dormant season salt applications were impacting the soil environment. I included plot identity as a random effect in the multi-year model using a linear mixed-effect model using the 'lmer' function of the 'lme4' package (version 1.1-32; Bates et al., 2015), and for models examining a single time point I used a linear regression model using the 'lm' function of the 'stats' package (R Core Team 2023) to model the effect of salt addition level on electrical conductivity. Salt treatment level was included as a fixed effect in all models.

## **Results**

Increased salt addition corresponded to increased soil salinity levels across all plots and years (Fig. 4.1; Table A4.2). The salt addition treatments elevated the soil electrical conductivity across all treatments early in the growing seasons (April and June), relative to unsalted plots, (Fig. 4.1; Tables A4.3-4.5). This effect tapered in the low to intermediate salt addition treatment

levels (25 g/m<sup>2</sup> - 50 g/m<sup>2</sup>) compared to the unsalted plots, but the effect remained for the high levels of salt addition as compared to the unsalted plots by the end of each growing season (Fig. 4.1; Tables A4.6-4.7).

During both the first and second growing season, plant community composition was significantly structured by the salt addition treatment (Fig. 4.2; Tables A4.8-4.9). Neither seed source, nor the interaction between salt treatment level and seed source, were significant predictors of plant community composition during either growing season.

During the first growing season, intermediate to high levels of salt addition (50 g/m<sup>2</sup> -100 g/m<sup>2</sup>) reduced seeded species cover (Fig. 4.3a; Table A4.10), but non-seeded species cover was not influenced by either seed source, salt treatment, or the interaction of these factors (Fig. 4.3c; Table A4.10). During the second growing season, many of the same patterns were observed for seeded species cover (Fig. 4.3b, 4.3d; Table A4.11). However, in the second growing season seeded species cover was reduced by all levels of salt addition, not just intermediate to high levels (Fig. 4.3b; Table A4.11).

Seeded species richness during the first growing season was influenced only by the interaction between seed source and one salt addition level  $(75 \text{ g/m}^2)$ ; Table A4.12), resulting in lower seeded species richness when coastal genotypes were included, than when only Midwest genotypes were included (Fig. 4.4a). Similarly, seeded species richness was again influenced by the interaction between seed source and one salt addition level (75 g/m<sup>2</sup>; Table A4.13) in the second growing season resulting in lower seeded species richness when coastal genotypes were included, than when only Midwest genotypes were included (Fig. 4.4b). Additionally, during the second growing season seeded species richness was also reduced by some salt addition levels (50  $g/m^2$  and 100  $g/m^2$ ; Fig. 4.4b; Table A4.13).

All levels of salt deposition reduced the total count of seeded species compared to the control treatment, and there was a progressive reduction in seeded species counts with increasing salt treatment levels during the first growing season (Fig 4.5a; Table A4.14). Additionally, there were lower counts of seeded species, when sourced from the coastal seed source (Fig. 4.5a; Table A4.14). Counts of several seeded species, like *Rudbeckia hirta* and *Coreopsis lanceolata*, were reduced at all salt treatment levels, and there was a progressive reduction in counts with salt treatment level (Fig. 4.5b, 4.5c; Tables A4.15-4.16). There were fewer counts of *C. lanceolata* in the coastal seed source treatment overall (Fig. 4.5c; Table A4.16), with some evidence for this

same effect in *R. hirta* though only significantly at a high level of salt addition (75  $g/m^2$ ; Fig. 4.5b; Table A15). Counts of *Potentilla arguta*, for which seed source was not manipulated, were negatively correlated with an intermediate level of salt addition  $(50 \text{ g/m}^2; \text{Fig. 4.5d}; \text{Table}$ A4.17). Whereas counts *Verbena stricta,* which was also not included in the seed source treatment, were not impacted by the salt addition treatments (Fig. 4.5e; Table A4.18). **Discussion**

I found clear evidence that establishing prairie plant communities were altered by salt deposition. Overall, the plant community composition was shaped by salt deposition, and this seemed to stem predominantly from seeded prairie species responses; seeded prairie species experienced reductions in cover, richness, and rates of establishment in response to salt deposition. On the other hand, non-seeded species cover was non-responsive to all salt deposition treatment levels. Seeded species sourced from coastal populations did not establish better than species sourced from Midwestern populations in terms of cover, richness, or rates of establishment and there is some evidence that they established worse than the Midwestern sourced species. Individual species varied in their responses to salt deposition, but all levels of salt deposition had clear detrimental effects.

A key finding of this study was that salt reduced the richness and cover of seeded prairie species, whereas the cover of non-seeded species was unaffected by salt. Previous work has shown similar differential detrimental effects of salt deposition on native and non-native plant community members as a result of higher salt sensitivity in native plant species, particularly at the germination stage, than some non-native plant species (Dudley et al., 2014; Fischel, 2001). Multiple non-mutually exclusive mechanisms may have contributed to these effects, including both direct impacts of salt deposition like, disrupting the availability of water in the soil for germinating seeds and established plants (Ambika et al., 2016; Ryan et al., 1975) and indirect effects like altering rates of decomposition in the rhizosphere leading to reduced soil organic matter and fertility (Ambika et al., 2016; Buckland & Grime, 2000). Overall, due to salt sensitivity many native plant species typically fail to germinate, or are unable to persist, in salt impacted roadside soils and are then often replaced by more salt tolerant non-native species like *Daucus carota* (wild carrot) or *Ambrosia artemisiifolia* (common ragweed; Environment Canada and Health Canada, 2001). Thus, even though I found that prairie species were able to establish at all salt levels, increasing levels of salt deposition may favor a relatively more weed dominated

community, due to progressive reductions in the germination and establishment of seeded prairie species.

Contrary to my hypothesis, the inclusion of coastal genotypes within the seed mix did not mitigate the effects of repeated salt deposition. Although previous work has shown adaptations to salty conditions may exist within species, especially when a species' distribution includes coastal regions (Busoms et al., 2023; Itoh, 2021; Lowry et al., 2008), and thus may be naturally adapted to roadside conditions, I did not find evidence of this in this study. In fact, in some instances coastal genotypes established at lower rates than Midwestern genotypes (Fig. 4.5). Coastal genotypes may have established at lower rates than Midwestern genotypes for several reasons. For instance, coastal genotypes were sourced from a non-local region thus they may not have been as locally adapted to other unmeasured conditions at the planting site as Midwestern genotypes (i.e., Hereford, 2009). So, even if coastal genotypes were locally adapted to salt deposition, this effect may have been overshadowed by negative consequences of non-local adaptation to the planting site in general. This study suggests that local seed sources are likely sufficient, and in some cases may be better suited due to local adaptation to other environmental conditions not tested for in this study, for roadside restoration despite the altered abiotic conditions found along roads.

When considered together, seeded species were able to establish in all salt treatments but showed reduced rates of establishment in response to increasing rates of salt deposition. Even for the best establishing seeded species, there was a clear detrimental effects of salt deposition on rates of establishment. This is likely tied to reductions in germination of seeded species in the face of increasing salt deposition and accumulation in the soil (Dudley et al., 2014; Fischel, 2001; Ryan et al., 1975). However, despite this some seeded species were able to establish at higher rates than others across all salt deposition levels. For instance, *R. hirta* and *C. lanceolata,*  forb species that are commonly seeded into prairie restoration plantings, established in high numbers across all salt treatment levels. Whereas other seeded species that are also commonly included in prairie restoration efforts such as *Chamaecrista fasciculata* and *Echinacea purpurea*  established at low levels across most salt deposition treatments. Despite the low rates of establishment for many of the seeded species during the first growing season, during the second growing season, seeded species richness was slightly higher at low to intermediate levels of salt deposition (Fig. 4.4a, 4.4b). This may indicate that better establishing seeded prairie species

could be facilitating autogenic recovery of the soil. Autogenic recovery is the process by soil conditions gradually improve through a positive feedback loop of plant growth and senescence (Whisenant, 1999), and has been proposed as a tool for enhancing the establishment of native plant communities along roadsides (Blanchard et al., 2023).

This study provides experimental evidence that salt deposition is an agent of roadside plant community change. There were clear negative effects of salt deposition on prairie plant community establishment as a whole and even for the best establishing species, and these effects were not mitigated by sourcing seed from coastal populations. This study indicates that local seed sources are likely sufficient, and in some cases may be better suited due to local adaptation to other environmental conditions not tested in this study, for roadside restoration as compared to coastal seed sources. These results suggest that the inclusion of native prairie species able to establish at higher rates of salt deposition in addition to targeting areas with low to intermediate salt deposition rates will likely improve the establishment of a diverse prairie plant community with low establishment of non-seeded weedy species.

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# FIGURES

Figure 4.1 Average electrical conductivity (mS/cm) with standard deviation within each salt addition level across growing seasons. Salt treatment level is indicated by color ranging from the control treatment to the highest salt treatment level.



**Figure 4.2** Plant community data from the 2023 growing season using a non-metric multidimensional scaling (NMDS) ordination using the Bray Curtis dissimilarity metric. Seed source treatment is indicated by shape, circles indicate the inclusion of seeds sourced from both the Midwest and coastal seed producers and triangles indicate the inclusion of only seeds sourced from the Midwest producer. Salt treatment level is indicated by color ranging from the control treatment to the highest salt treatment level. Stress = 0.22.



**Figure 4.3** Average cover with standard deviation of seeded (a-b) and non-seeded species (c-d) within each salt addition level and seed source treatment across growing seasons. **a)** average seeded species cover during the first growing season **b)** average seeded species cover during the second growing season **c)** average non-seeded species cover during the first growing season **d)** average non-seeded species cover during the second season. Color indicates seed source treatment: black indicates the inclusion of seeds sourced from the Midwest seed producer only (MW) and gray indicates the inclusion of seeds sourced from both the Midwest and coastal seed producers (MC).



**Figure 4.4** Average richness with standard deviation of seeded and non-seeded species within each salt addition level and seed source treatment across growing seasons. **a)** average seeded species richness during the first growing season **b)** average seeded species richness during the second growing season. Color indicates seed source treatment: black indicates the inclusion of seeds sourced from the Midwest seed producer only (MW) and gray indicates the inclusion of seeds sourced from both the Midwest and coastal seed producers (MC).



**Figure 4.5** Plots of seeded species counts during the first growing season. **a)** average of summed seeded species with standard deviation **b)** average count with standard deviation of *Rudbeckia hirta* within each salt treatment level **c)** average count with standard deviation of *Coreopsis lanceolata* within each salt treatment level **d)** average count with standard deviation of *Potentilla arguta* within each salt treatment level **e)** average count with standard deviation of *Verbena stricta* within each salt treatment level. Black indicates seed was sourced from the Midwestern seed producer (MW) and grey indicates seed was sourced from the coastal seed producer (MC).



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# APPENDIX

Table A4.1 List of species included in the seed mix. Species indicated with an asterisk (\*) were sourced from both Native Connections, Kalamazoo, MI and Pinelands Nursery Columbus, NJ.





**Table A4.2** The output of a linear regression model evaluating how salt treatment level influences the electrical conductivity of the soil across years with plot identity as a random effect.

**Table A4.3** The output of a linear regression model evaluating how salt treatment level influences the electrical conductivity of the soil during June 2022.





**Table A4.4** The output of a linear regression model evaluating how salt treatment level influences the electrical conductivity of the soil during June 2023.

**Table A4.5** The output of a linear regression model evaluating how salt treatment level influences the electrical conductivity of the soil during April 2023.





**Table A4.6** The output of a linear regression model evaluating how salt treatment level influences the electrical conductivity of the soil during August 2022.

**Table A4.7** The output of a linear regression model evaluating how salt treatment level influences the electrical conductivity of the soil during August 2023.





**Table A4.8** The output of a PERMANOVA model evaluating how seed source and salt treatment level influence plant community composition during the first growing season using the Bray-Curtis dissimilarity metric.

Table A4.9 The output of a PERMANOVA model evaluating how seed source and salt treatment level influence plant community composition during the second growing season using the Bray-Curtis dissimilarity metric.




**Table A4.10** The output of a linear regression model evaluating how seed source and salt treatment level influence the cover of seeded and non-seeded species pooled to the plot level during the first growing season.



**Table A4.11** The output of a linear regression model evaluating how seed source and salt treatment level influence the cover of seeded species pooled to the plot level during the second growing season.



**Table A4.12** The output of a linear regression model evaluating how seed source and salt treatment level influence the richness of seeded species pooled to the plot level during the first growing season.



**Table A4.13** The output of a linear regression model evaluating how seed source and salt treatment level influence the richness of seeded species pooled to the plot level during the second growing season.



**Table A4.14** The output of a linear regression model evaluating how seed source and salt treatment level influence the counts of all seeded species pooled to the plot level during the first growing season.



Table A4.15 The output of a linear regression model using the negative binomial distribution evaluating how seed source and salt treatment level influence the counts of a seeded species, *Rudbeckia hirta*, during the first growing season.



Table A4.16 The output of a linear regression model using the negative binomial distribution evaluating how seed source and salt treatment level influence the counts of a seeded species, *Coreopsis lanceolata*, during the first growing season.



**Table A4.17** The output of a linear regression model using the zero inflated Poisson distribution evaluating how seed source and salt treatment level influence the counts of a seeded species, *Potentilla arguta*, during the first growing season.



**Table A4.18** The output of a linear regression model using the negative binomial distribution evaluating how seed source and salt treatment level influence the counts of a seeded species, *Verbena stricta*, during the first growing season.