PLANTING YEAR CONDITIONS SHAPE COMMUNITY ASSEMBLY IN RESTORED PRAIRIE COMMUNITIES

Ву

Anna Marjorie Groves

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ABSTRACT

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By

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This dissertation focuses on the influence of planting conditions on the restoration of prairie communities, both in the applied context of improving restoration outcomes, and as a test of our understanding of mechanisms of community assembly. Ecological restoration is incredibly important in this era of human-induced landscape degradation, but restoration projects do not always result in outcomes that match practitioners' goals. A possible factor in this variation is the weather conditions that occur at the outset of a restoration project that are typically referred to as "year effects." However, we lack strong tests of year effects that disentangle them from site-to-site variation and other confounding factors, such as management. Additionally, there has been no investigation of the mechanisms for year effects; current evidence for this phenomenon is correlational and lacks direct experimentation. Inter-annual variation in precipitation is often assumed to be a major factor causing year effects, though there are countless potential drivers that could vary inter-annually. In addition to implications for restoration, evidence for year effects would suggest assembly is driven by stochastic mechanisms (i.e. random variation due to weather) as opposed to deterministic mechanisms (i.e. drivers with consistent, repeatable effects such as site soil characteristics or prescribed fire management).

To address these challenges, I investigated the causes and consequences of planting-year variation on community assembly in a tallgrass prairie restoration system using two main methods: (I) an experimental manipulation of precipitation as part of a long-term prairie restoration at Michigan State University's W. K. Kellogg Biological Station (KBS), and (II) an analysis of differences in species composition among 83 restored tallgrass prairies established in different years across the Midwestern United States of America. I first explored how year effects on seedling emergence and survival. I created 6 replicate prairies in three different years, using identical methods at a single large site. In each year, experimental plots within each restored prairie received water manipulation treatments for the first nine weeks after sowing. In these plots, rainfall was blocked with rain-out shelters and then watered low (1.39 cm/month), mean (9.91 cm/month), or high (17.81 cm/month) amounts compared to the 30-year average in the area. I found large differences in seedling emergence across the three planting years as well as across watering treatments. Initial community composition differed across years but not watering treatment. I continued to monitor these communities to determine if initial differences would persist. I found that some initial community differences dissipated while others persisted, suggesting the operation of both deterministic and stochastic assembly mechanisms in this system.

In the second study, I looked for year effects in existing restored prairies across a wide geographic and temporal range. In summer 2016, colleagues and I visited 83 prairies in Illinois, Indiana, and Michigan that had been restored between 2000-2015 and determined their current plant community compositions. Using these data, I evaluated the importance of planting conditions using historical weather data on restoration outcomes, also accounting for different management histories and locations. I found that planting year precipitation had lasting effects on the richness and abundance of non-sown species. These signatures explained as much variation in the community as known drivers of assembly such as soil characteristics, fire frequency, and seed mix richness. These data provide additional support that planting year conditions can have profound effects on communities in sown restoration projects which can persist through assembly over time. Documentation of persistent year effects will be helpful for understanding the mechanisms that drive variation in restoration outcomes and could be used to inform tailored remedial management that addresses contingencies that arise after different first year conditions. For Andy

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CHAPTER ONE

PLANTING YEAR EFFECTS IN RESTORATION

"If the science can't predict the outcome of a restoration effort with some confidence, it clearly has a long way to go." -John Cairns, 1987

INTRODUCTION

What's in a planting year? Any farmer or restoration practitioner might tell you, a lot. Weather happens, and weather affects plants. But can weather events in one important year shape a plant community for the long term? How much do planting conditions influence efforts to restore ecological communities that have been degraded or destroyed?

Ecological restoration has the potential to slow or reverse the loss of global biodiversity, whose greatest threat is the alteration of ecosystems for human land use (Foley et al. 2005; Cardinale et al. 2012). Restored systems, like the natural systems they strive to emulate, can provide many functions and services that benefit humankind such as habitat for crop pollinators, storm water filtration and retention, or carbon sequestration (Dobson et al. 1997; Choi 2007; Bullock et al. 2011). But this recovery of biodiversity and provisioning of ecosystem services relies on the success of restoration practitioners in meeting their goals; for instance, establishing the intended community. In reality, restoration outcomes can vary widely and often differ from goals (Hobbs & Norton 1996; Matthews & Spyreas 2010; Suding 2011). A better understanding of the determinants of restoration outcomes is essential to achieve the expected benefits of restoring native ecosystems.

Ecological restoration is often focused on re-establishing native plant communities to restore the functionality of the target system (Ruiz-Jaen & Mitchell Aide 2005; Brudvig 2011). Successful restoration therefore requires a clear understanding of the structure of the target community (e.g.,

relative abundances of desired species) as well as methods for establishing this community in context of the current conditions at a particular site. Ecologists have been striving to understand the processes that drive the establishment and structure of communities for over a century (Cowles 1899; Clements 1916; Weiher et al. 2011); therefore, ecological theories on how communities assemble should be able to inform restoration practices aimed at reassembling native communities (Palmer et al. 1997; Young et al. 2001, 2005). Restoration, in turn, provides opportunities to test theories of how ecological communities assemble, under different field settings (Bradshaw 1987). Multiple ecological theories, invoking a variety of mechanisms such as ecological filters (Belyea 2004), assembly rules (Diamond 1975, Weiher and Keddy 1995), and succession (Pickett et al. 2001; White & Jentsch 2004) have been advanced to explain patterns of community assembly in restoration (e.g., Temperton et al. 2004). However, the continued unpredictability of restoration outcomes implies that no currently implemented theory provides a fully workable understanding of how communities assemble during restoration.

Historically contingent assembly models

A missing consideration in these models of community assembly may be the way in which the development of a community, or its history, can affect the subsequent community state (e.g., Drake 1991). These ideas can be traced back to early assembly models where "accidents" of seed dispersal were more important than the overall system (Gleason 1926) and where initial floristic composition shaped communities (Egler 1954); they also have strong parallels to theories of succession (e.g., Connell & Slatyer 1977). These historically contingent assembly models, in which communities are structured by events such as the arrival order of species during assembly, are now prevalent in the community assembly literature (Drake 1990; Law & Morton 1993; Chase 2003; Fukami et al. 2005), but have received relatively little attention in a restoration context (Brudvig 2011). Microcosm experiments and computer simulations modeling temporal events that could affect community assembly have indicated

that the identity of community members early in assembly can affect later community composition, even when early community members do not persist in the community (Lockwood & Samuels 2004). Species that become established early can also have a greater chance of remaining competitively dominant than later arrivers (i.e. "priority effects", Alford and Wilbur 1985). It follows that different ecological communities can develop under otherwise identical environmental conditions due to differences in the order in which species colonize a space (Gleason 1926; Egler 1954; Sutherland 1974; Robinson & Edgemon 1988; Fukami et al. 2005).

This case for historically contingent assembly seems particularly strong for restoration projects that are initiated through a single sowing (e.g., most tallgrass prairies), as many environmental factors that could impact seedling emergence and survival are highly variable from year to year. For these communities, temporally variable abiotic or biotic conditions such as temperature, precipitation, competitive dynamics, or predator pressures may control establishment order by favoring or disfavoring species at this critical early stage of the assembly process. Some evidence has shown that inter-annual environmental variation during the first growing season of a restored community can have persistent effects both in restoration projects (Bakker et al. 2003; MacDougall et al. 2008; Stuble et al. 2017) and ecological experiments in general (Johnson 2002, reviewed in Vaughn and Young 2010), but the full scope of these effects remains unclear because few studies of experimental restoration are replicated across years (Vaughn & Young 2010). As a result, much evidence for year effects on restoration outcomes is correlational and confounded with differences in management practices (e.g., seed mix diversity/composition) and site-specific conditions (e.g., edaphic conditions). To better understand variation in the composition of restored communities and increase our understanding of the importance of historically contingent assembly models, we need empirical evidence to determine how and when establishment history, and specifically year effects, influence community assembly and restoration outcomes.

Testing year effects in restored communities

For my dissertation, I investigate the effects of planting year conditions on restored plant communities. Throughout, I evaluate the interaction between year effects and a major management decision for prairie restoration practitioners: the richness of the seed mix. In the chapters that follow, I examine: (I) mechanisms that shaped plant establishment in three planting years in an experimental restored community; (II) whether differences from the first growing season in these experimental communities persisted over time; and (III) the relative importance of planting year weather conditions for restored prairies of various ages and management histories across the Midwest. These three chapters provide three important lines of evidence that together make for a strong test of whether year effects, disentangled from site, management, and other factors, are important drivers of variation in restoration outcomes.

In chapter 2 of this dissertation, I examined mechanisms of year effects. Evidence is needed to demonstrate that year effects occur without confounding factors and to elucidate the conditions and subsequent processes that could cause a year effect. For instance, warmer temperatures, especially in early mornings or springtime, can advance the phenology of some plant species (Forrest & James 2011), which can favor certain species over others (Wainwright & Cleland 2013). Precipitation, too, has known impacts on plant communities (Silvertown et al. 1999; Robinson & Gross 2010). Populations of rodents can fluctuate between years (e.g., Getz and Hofmann 1999), which can in turn impact the establishing plant community through post-dispersal seed predation (Hulme & Kollmann 2005; Notman & Villegas 2005) or herbivory (Howe & Brown 1999; Howe 2008; MacDougall & Wilson 2007). Knowing the extent to which temporal variation in environmental factors impact community assembly during restoration has obvious practical significance, especially when coupled with an understanding of the actual process by which the plant community is affected (e.g., whether the condition affects germination, seedling survival, or adult growth). To address this in my second dissertation chapter, I established experimental

prairie plots in three planting years, using identical methods. In each year, I established three rainfall treatments, spanning the historical levels of precipitation in this area over the past 30 years (record low, 1.39 cm/month; mean, 9.91 cm/month; and 93rd percentile, 17.81 cm/month). The goal was to disentangle to effects of inter-annual precipitation—my leading hypothesis— from other factors that may vary annually. I tracked seedling emergence and survival in the first growing season in each year to determine whether seedling emergence or survival is most affected by conditions at the time of planting, and finally compared the composition of the communities that developed in each first growing season. This investigation of the planting-year community provides a mechanistic explanation for how year effects could be introduced to a restored community.

To determine what, if any, differences in the early community persist over time, I monitored the community composition of the experimental prairie plots outlined above for an additional 1-3 years (depending on planting year). These results are reported in Chapter 3. If the communities that developed in subsequent years remained different over time, then this provides evidence that assembly is historically contingent, and year effects can impact longer-term restoration outcomes. Otherwise, the communities will have converged (i.e. become more similar) through time regardless of initial differences, due to the shared conditions (e.g. soils, invasive species pressures, and management), supporting a deterministic assembly model in which year effects do not impact restoration outcomes.

Because the above experiment was conducted at a single site in Michigan, a critical final consideration is whether there are detectable effects of initial planting conditions on real restored prairie sites across the Midwest. To address this question, in my fourth dissertation chapter, I report results from field surveys of 83 restored prairies located across the Midwest, ranging in age from 2-19 years old. At each site I collected data on soils (e.g. water holding capacity, nutrient composition) and management histories (e.g. seed mix sown, prescribed fire history) and determined first growing season weather conditions using PRISM online database. This allowed me to evaluate the effect of first growing

season planting conditions on the present-day plant community, with interest in their effects relative to other factors known to structure assembling restoration communities.

Finally, the impact of a year effect may vary depending on the specific methods used to establish a restoration in the first year, especially the species richness of the seed mix used. Sowing a higher richness seed mix may buffer against adverse year effects; that is, the impact of poor planting year conditions on restoration success may be less in high than in low diversity prairies. This buffering would occur when a greater selection of species increases the likelihood that a seed mix includes species that can establish given the specific environmental conditions (i.e., through a portfolio/insurance effect, Tilman and Downing 1994, lves et al. 1999, Tilman et al. 2006, Hector et al. 2010). If the species richness of seed mix does not interact with a year effect, the community should more closely resemble targets (i.e., higher native cover and diversity—common metrics of restoration success) in high than in low diversity plantings regardless of initiation year. I address this question throughout my dissertation; by crossing a high and low richness seed mix throughout my experiment, and by considering the richness of the seed mixes sown throughout the sampled Midwestern prairies in their analysis.

Study system

I conducted the above restoration experiments and observational studies in a tallgrass prairie restoration system. Nearly 99.9% of native prairie has been lost since European settlement of North America, making this system a high priority for restoration (Samson & Knopf 1994). Decades to centuries of intensive agriculture on most former prairie sites has resulted in a complete loss of remnant prairie species in the seed bank or in the landscape that could naturally recolonize a site following agricultural abandonment, therefore prairie restoration projects require seed sowing to establish new communities (Thompson et al. 1998; Suding & Gross 2006; Cramer et al. 2008). This restoration by seed sowing allows for explicit manipulation of arrival order of species to a community. The fine-scale community size of a

prairie, plus the relatively fast maturation and manageable size of prairie plants, combine to make prairies a prime system for experimentation with community assembly mechanisms (Jordan 1997, e.g., Foster et al. 2007, Dickson et al. 2012, Martin and Wilsey 2012). Prairie restoration research can therefore be beneficial both to basic ecological knowledge as well as to active conservation practice. LITERATURE CITED

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CHAPTER TWO

INTER-ANNUAL VARIATION IN PRECIPITATION AND OTHER PLANTING CONDITIONS IMPACTS SEEDLING ESTABLISHMENT IN SOWN PLANT COMMUNITIES

ABSTRACT

Ecological restoration can reverse biodiversity loss worldwide, yet restoration goals and outcomes vary widely, which limits this potential. Divergent restoration outcomes may stem from variation in conditions at the outset of restoration, but empirical evidence is lacking and typically confounded with site differences. Additionally, precipitation is usually cited as the source of this variation, although a wide range of conditions can vary annually. We tested for effects of planting year on seedling establishment by installing identical restorations in three different years. Within those years, we manipulated rainfall with rain-out shelters to disentangle the effects of precipitation from other annually variable conditions. Additionally, we tested whether increasing seed mix richness buffers against adverse planting conditions. For the first growing season after planting, we followed emergence and survival of sown prairie species and non-sown weed species to determine how planting year conditions influence an establishing plant community, if at all. We found that seedling establishment differed across planting years and precipitation treatments, and that varying emergence patterns by species led to differences in the composition of the first-year community. We also found significant variation in sown species establishment across years when precipitation was held constant, illustrating the previously overlooked role of non-precipitation drivers on planting year effects. Higher seed mix richness did not consistently improve establishment of sown species under different planting conditions. This research provides important experimental evidence for effects of inter-annual variation in planting conditions on first-year establishment. Future work will examine how these initial changes affect longerterm assembly dynamics.

INTRODUCTION

The greatest threat to global biodiversity is the alteration of ecosystems for human land uses (Foley et al. 2005; Cardinale et al. 2012). Ecological restoration has the potential to slow or reverse biodiversity loss in human-impacted ecosystems and landscapes (Dobson et al. 1997; Choi 2007; Bullock et al. 2011); however, this recovery is reliant on restoration efforts achieving these goals (Rowe 2010). For instance, ecological restoration often focuses on rebuilding plant communities to promote ecosystem functionality (Ruiz-Jaen & Mitchell Aide 2005; Brudvig 2011), yet restoration outcomes vary widely and often differ from goals (Hobbs & Norton 1996; Matthews & Spyreas 2010; Suding 2011). A critical step toward development of more predictably successful restoration practices is understanding the factors determining restoration outcomes (Brudvig et al. 2017).

Variation in restoration outcomes may result from the numerous ways that restored sites differ from one another (e.g., soils, landscape context, etc.; e.g., Grman et al. 2013). However, a critical realization is that outcomes may differ among otherwise similar or even identical sites due to differences in environmental conditions at the outset of a restoration effort. These "year effects" relate to historically contingent theories of community assembly (Fukami 2015). For instance, microcosm experiments and computer simulations modeling temporal events that could affect community assembly have indicated that the identity of community members early in assembly can affect later community composition, either by remaining competitively dominant over later arrivers (i.e., "priority effects," Shulman et al. 1983) or for other reasons even when early establishers do not persist in the community (Lockwood & Samuels 2004). The implication for restoration is that conditions favoring the establishment of particular species early in restoration may subsequently influence the composition of the restored community (Young et al. 2001; Brudvig 2011; Miller et al. 2016).

In practice, understanding the influence of year effects on restoration is limited for several reasons. First, although agronomic studies are commonly replicated across years (Vaughn & Young 2010), there is limited evidence for year effects in restoration and ecological experiments in general (Johnson 2002; Bakker et al. 2003; MacDougall et al. 2008; Young et al. 2015; Wilson 2015; Stuble et al. 2017), because it is rare that restoration projects or ecological experiments are replicated across years (Vaughn & Young 2010). Second, most studies have evaluated year effects in restoration by comparing sites established in different years, resulting in confounding of years with differences in management practices (e.g., seed mix richness/composition) and site-specific conditions (e.g., edaphic factors). As such, results interpreted as year effects may in fact be management or site effects. Third, we currently have little understanding of the mechanisms underlying year effects. Previous studies have correlatively linked year effects with variable rainfall patterns (Bakker et al. 2003; MacDougall et al. 2008; Stuble et al. 2017); however, year effects could result from numerous factors spanning variation in rainfall, temperature, consumer abundances and identities, the abundances of competitors of focal restoration species, and many others. For instance, MacDougall et al. (2008) planted grassland species across multiple years in a restoration experiment, and found that 10 years later, plots sown in two normal precipitation years were dominated by natives, while plots seeded in a single dry year reverted to dominance by exotics. Although this relationship with planting-year precipitation is plausible, conditions in addition to precipitation could have varied across those years or sites.

We tested for year effects in an experiment that controlled for site effects and manipulated the leading putative cause of year effects— inter-annual variation in precipitation. Specifically, we established sown prairie plots at a single site, using identical methods in each of three years. Within these plots, we manipulated precipitation during the planting year, resulting in plots established under identical amounts of precipitation, but in different years. This approach provided a strong test of precipitation as a determinant of year effects and, at the same time, considered the influences of non-

precipitation causes of year effects (i.e., inter-annual variation not explained by the precipitation treatment).

Our work also considered whether year effects might interact with aspects of management. In some restorations, all target species are sown at the same time, with a goal of maximizing sown species establishment while suppressing non-sown community members. In these systems, the plant community that establishes will be determined by the practitioner's methods as well as the environmental conditions after sowing. Increasing the species richness of the seed mix is expected to increase the number of species suited to respond favorably to the environmental conditions of any given year (Tilman et al. 2014; Isbell et al. 2015) and therefore increase the overall establishment of target species. This should be particularly important under harsh conditions such as insufficient precipitation (Chase 2003), which may preclude establishment of many species. We therefore considered the role of propagule addition in our study, investigating whether a greater diversity of seeds used to establish a plant community would buffer against adverse year effects and allow for greater establishment of sown species.

Finally, there is contradictory evidence for whether emergence versus seedling survival is most likely to limit establishment in sown systems and determine a species' presence in the plant community. For example, in an arid grassland system, sown plant recruitment was limited by a bottleneck between germination and emergence (James et al. 2011), while Turnbull et al. (2000) found in a meta-analysis across systems that most establishment was limited at the transition from seedling to adult. Additionally, the ecologically relevant conditions that break seed dormancy and cue germination are highly dependent on climate (Walck et al. 2011), and sometimes the conditions favoring germination do not in turn favor the survival of seedlings (Lloret et al. 2009). Understanding the responses of target (sown) and non-target (non-sown) plants in restoration at these demographic transitions has important ramifications for management. For instance, if emergence rates and seedling mortality are high under

certain conditions, this would deplete the pool of sown propagules and managers should prepare to resow certain restoration projects. In this way, responses of individual species to different planting conditions could determine the composition of the first-year community. This, in turn, may influence the composition of subsequent years, even when the first-year community does not itself resemble the later community.

Empirical evidence is needed to clearly disentangle the mechanisms by which precipitation and other factors that vary inter-annually influence the establishment of a sown restoration. This research addressed four main questions: (1) Do emergence and/or seedling survival vary in different planting years? We predicted significant variation in the emergence and survival of seedlings across three planting years. (2) Do these processes vary due to precipitation, or non-precipitation conditions? We expected both seedling emergence and survival to increase with increasing precipitation after planting. (3) What is the influence of sown species richness on the above processes? We hypothesized a higher seed mix richness to buffer against adverse planting conditions, leading to higher seedling establishment. Finally, (4) do different planting conditions result in different first-year communities? We predicted variation in species responses to planting year conditions and precipitation treatments would result in different composition of first-year communities. For each of these questions, we considered sown and non-sown species separately, owing to their different impacts on restoration outcomes and potential for these two groups to respond differently to planting year effects.

METHODS

Study site and restoration methods

This experiment was conducted at Michigan State University's Kellogg Biological Station, at the Lux Arbor Reserve near Prairieville, MI. Tallgrass prairie was a historical ecosystem type in this region

and restored prairies are prevalent in this region (Grman et al. 2014). The site was historically mixed-oak savanna (Comer et al. 1995), was cleared for cultivation prior to 1946, used as a private air-strip in the 1960s and 1970s, abandoned sometime before 1980, and has been mowed approximately annually to prevent woody encroachment. Before this experiment, vegetation at the site closely resembled other abandoned fields in the area, and was dominated by *Bromus inermis* (Smooth brome), *Centaurea stoebe* (Spotted knapweed), and other exotic and native weedy perennials.

We converted a subset of this abandoned field to prairie in each year (2014-2016) of the experiment. Each May, we mowed plots to stimulate growth, sprayed vegetation with glyphosate herbicide, tilled, hand broadcasted native prairie seeds, and packed with a cultipacker to increase soil-seed contact and probability of germination. We cultipacked on 19-20 May each planting year.

Experimental design

To test how restorations are impacted by planting year conditions, precipitation treatment, and seed mix richness, we utilized a randomized complete block design (n=6 for each year by precipitation by seed mix treatment, 24 combinations total, **Figure 2.1**). We installed six replicate prairie blocks (15.2 m x 36.6 m) in three planting years (2014-2016); each sown with a baseline low richness prairie mix (8 species, 379 seeds/m²) to serve as a buffer around experimental plots. Within each block, we installed four experimental plots (1.0 m x 0.5 m), to which four whole-plot factor treatments (ambient conditions; low, mean, and high precipitation) were randomly assigned.

Finally, each experimental plot was split, with each half (0.5 m x 0.5 m) receiving additional seeds of either a high or low richness seed mix. The low richness plot received an additional 379 seeds/m² of the 8 species mix already sown across the entire block (total sown density, 758 seeds/m²). The high richness plot received 379 seeds/m² of a 22 species mix, bringing total sown richness to 30 species (total sown density, 758 seeds/m²). We chose species for the seed mixes that were typical of

low- and high-diversity plantings in this region. The high and low richness seed mixes contained the same proportions of seeds from different life-form groups (i.e., forb, legume, C3 grass, C4 grass). Due to a seed supplying error, 2016 plots were sown with *Echinacea pallida* instead of *E. purpurea*; these two species have been combined for analysis, though no *Echinacea* emerged in 2016. Each species was tested for viability each year by the seed supplier and mixes were adjusted such that each planting received the same quantity of live seed (**Table 2.1**).

Precipitation treatments

In order to simulate drought, normal, and wet year conditions relevant for this field site, we used the 30-year monthly averages for May-July from the nearest weather station (Gull Lake, MI, 10 km from field site) to determine frequency (8 days/month) and quantity of watering. The three treatments were based on: the record low (1.39 cm = 13.8 L/m^2 monthly), the 30-year mean (9.91 cm = 99.1 L/m^2 monthly), and the 93^{rd} percentile (17.81 cm = 178.1 L/m^2 monthly). Precipitation treatments were rounded to the nearest gallon to facilitate compatibility with the watering cans used.

To implement precipitation treatments, we diverted and collected all rainfall from the experimental plots for the first nine weeks after sowing using rain-out shelters (**Figure 2.8**). To meet precipitation treatments, rainwater was supplemented with well water. Frequency of water application was held constant throughout the treatment period (two times/week; every 2-5 days); all treatments were watered on the same day. We installed rubber gardening edging around experimental plots to prevent overland flow of water in the precipitation treatment plots and to permanently mark the plots. Sediment collecting on rain-out shelters reduced light availability by $19 \pm 1\%$ by the end of July when shelters were taken down each year. Although rain-out shelters may have had impacts on plot-level microclimate (e.g. slightly increasing temperature through greenhouse effects), this is not a concern for

interpreting precipitation treatment results since all plots would have been similarly affected and plots with and without rain-out shelters are treated separately in all statistical analyses.

Seedling and plant community surveys

We conducted plant surveys in the plots that were sown each year (2014-2016) to examine how seedling emergence, seedling survival, and the first-year community varied in different planting years, precipitation treatments, and levels of seed mix richness. Within each experimental split-plot, three 10 x 10-cm sub-sampling plots were permanently marked and individual seedlings were marked with color-coded sewing pins for week-to-week tracking. In 2014, seedling surveys were conducted weekly for the first nine weeks after sowing (30 May-24 July) to measure seedling emergence and seedling death rates of all sown and non-sown species in each sub-sampling plot. We used these data to determine the minimum sampling required to account for 87.5% of all seedlings, and thereafter surveyed 2015 and 2016 seedlings in weeks four (mid-June) and nine (late July) and subset 2014 data accordingly for all analyses. At peak growing season (late July) each planting year, we visually estimated percent cover of all species in each 0.5 x 0.5-m split-plot.

Finally, although all plots were mowed in late July of their planting year to prevent recruitment between planted areas and neighboring unplanted areas, a non-sown annual grass *Panicum capillare* set seed a second time after mowing and before the growing season was over. *P. capillare* therefore showed a marked increase in emergence with each subsequent planting year, making up 11.1% of all seedlings in 2014, 29.9% of all seedlings in 2015, and 71.2% of all seedlings in 2016. We believe this increase reflected increasing propagule pressure—an artifact of the experimental design—rather than a true year effect. We therefore conducted all analyses both with and without *P. capillare* included. We found that key results were consistent across the two methods; results presented here exclude *P*.

capillare (leaving 1966 total seedlings) in order to better represent true year effects, with differences noted in table legends. Results including *P. capillare* are available in **Table 2.2**.

Statistical analyses

We used generalized linear mixed models to examine the fixed effects of first-year precipitation treatment, planting year, and their interactions with sown richness on the emergence and survival of all sown species, all non-sown species, and the three most abundant species from each of those two groups (separate models for each of these groupings; package "Ime4", Bates et al. 2015). For *D. ischaemum, B. curtipendula*, and *E. purpurea*, species models did not include interaction effects to allow for model convergence. Ambient plots were analyzed separately from rain-out shelter plots to test for naturally occurring planting year effects and to avoid confounding effects of rain-out shelter design. Models of sown species emergence used a binomial distribution to fit the number of seedlings and the number of non-emerged sown seeds. Models of seedling survival used a binomial distribution to fit the number of survivors and the number of deaths. All other emergence models used a Poisson distribution to fit the counts of seedlings. In models using ambient (no rain-out shelter) data, a random effect of block was added to control for heterogeneity across the experimental site; for rain-out data, a nested random effect of Block/Treatment was used. We compared within groups using Tukey adjusted post-hoc tests.

To test for community-level differences among planting year, precipitation treatment, and sown richness, we used permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) with Bray-Curtis dissimilarity and stratified by planting block (package "vegan," Oksanen et al. 2017). We used nonmetric multidimensional scaling (NMDS) in three dimensions also with Bray-Curtis dissimilarity to visualize differences in plant communities across planting years and precipitation treatments

(stress=0.19). All analyses were conducted in R version 3.3.2 (Fox and Weisberg 2011; Bates et al. 2015; R Core Team 2016).

RESULTS

A total of 3771 seedlings spanning 57 species were surveyed, of which 2860 were non-sown volunteers (38 species) and 461 were sown in this experiment (15 species). We were unable to identify 246 seedlings (6.5%) to species and therefore they were not classified as "sown" or "non-sown." An additional 204 individuals (5.4%) belonged to the genus *Elymus* which we dropped from the "sown" and "non-sown" analyses because we could not confidently distinguish between the sown *Elymus canadensis* and non-sown *Elymus repens* as small seedlings.

Ambient conditions

There was a year effect on seedling emergence and survival in plots exposed to ambient planting conditions. Sowing in three different years resulted in different emergence rates for both sown $(\chi^2_{(2,25)}=37.4, p<0.0001)$ and non-sown species $(\chi^2_{(2,28)}=37.5, p<0.0001)$. Sown prairie seedlings had 2.3 times higher emergence rates in 2015 (32.6% of seeds sown) than in 2014 (11.6% of seeds sown, *z*=-5.8, *p*<0.0001) or 2016 (16.7% of seeds sown, *z*=4.5, *p*<0.0001) (**Figure 2.2**). Similarly, non-sown species had 2.0 times emergence in 2015 than in 2014 (*z*=-4.5, *p*<0.0001) or 2016 (*z*=5.4, *p*<0.0001) (**Figure 2.2**). There was not a significant difference in emergence between 2014 and 2016 for sown (*z*=-1.4, *p*=0.35; however, when *P. capillare* included, *z*=-12.7, p<0.0001) or non-sown (*z*=1.0, *p*=0.55) species.

Seedling survival rates were high (93.6% of 608 seedlings survived in their first year in ambient plots (**Table 2.3**). Only 5 (of 168) sown seedlings died across all ambient plots in this experiment; therefore, statistical results are not presented. For non-sown species, total first year survival was

significantly different across years ($\chi^2_{(2,28)}$ =20.7, p<0.0001; however, when *P. capillare* included, $\chi^2_{(2,28)}$ =2.0, p=0.37). There was 2.6 times more seedling mortality in 2016 than in 2014 (*z*=-3.2, *p*=0.004) or 2015 (*z*=-4.1, *p*=0.0001). There was not a significant difference in non-sown seedling mortality between 2014 and 2015 (*z*=0.67, *p*=0.78).

There was a significant interaction between seed mix richness and planting year in ambient plots $(\chi^2_{(2,25)}=6.4, p=0.04, Figure 2.5a)$. The high richness mix led to 2.3 times more sown seedlings in 2016 (*z*=2.87, *p*=0.0041), but no significant difference between the two seed mixes in 2014 (*z*=-0.76, *p*=0.45) or 2015 (*z*=1.04, *p*=0.30). Full statistical results for the above are presented in Table 2.4.

Finally, there was a significant effect of planting year on community composition under ambient conditions (PERMANOVA: $F_{(2,17)}$ =1.9, p=0.004), because species varied in their emergence and abundance in different years (see Species Responses below).

Precipitation treatments

Precipitation treatment had a significant effect on seedling emergence of sown ($\chi^2_{(2,83)}$ =25.6, p<0.0001) and non-sown species ($\chi^2_{(2,84)}$ =19.0, p<0.0001) in rain-out shelter plots (**Figure 2.3**). As expected, more seedlings emerged as water increased; however, both groups only responded significantly to the increase from drought to average water levels (sown species, 2.3 times more emergence in mean than low treatment, *z*=-3.6, *p*=0.001; non-sown species, 1.9 times, *z*=-3.0, *p*=0.009). The strength of these effects on non-sown species varied with year ($\chi^2_{(4,84)}$ =39.4, *p*<0.0001), with significant effects of watering on emergence in 2015 and 2016 but not 2014 (**Table 2.5**). Seedling survival was not affected by precipitation treatment for sown ($\chi^2_{(2,80)}$ =1.17, *p*=0.56) or non-sown species ($\chi^2_{(2,80)}$ =5.91, *p*=0.05, **Table 2.3**).

Rain-out plots also exhibited a significant effect of planting year on sown seedling emergence, meaning there was still a year effect on sown species when precipitation was held constant across years

(i.e., differences existed among plots receiving the same rainfall treatment, but in different years; hereafter 'non-precipitation year effects') ($\chi^2_{(2,83)}$ =51.9, *p*<0.0001, **Figure 2.4**). Sown species emergence was again 2.2 times higher in 2015 than in 2014 (*z*=-5.7, *p*<0.0001) or 2016 (*z*=5, *p*<0.0001) under constant precipitation (**Figure 2.4a**). There was not a significant interaction effect between planting year and precipitation treatment on sown species ($\chi^2_{(4,83)}$ =3.21, *p*=0.52). Seedling survival of sown species did not vary across planting years ($\chi^2_{(2,80)}$ =1.85, *p*=0.40). The emergence of non-sown species was not affected by these non-precipitation year effects ($\chi^2_{(2,84)}$ =5.39, *p*=0.07, **Figure 2.4b**; however, when *P*. *capillare* included, $\chi^2_{(2,84)}$ =288.8, *p*<0.0001); however, the survival of these seedings varied across years ($\chi^2_{(2,80)}$ =12.6, *p*=0.002). The death rate of non-sown species was 3.1 times higher in 2014 than in 2015 (*z*=-3.3, *p*=0.003). Finally, there was a significant interaction between planting year and precipitation treatment on non-sown species emergence ($\chi^2_{(4,84)}$ =39.4, *p*<0.0001, **Figure 2.4b**). Within the low precipitation treatment, non-sown species emerged significantly more in 2014 than the other two years; within the mean treatment, 2016 had highest emergence; and for the high water treatment, 2015 had the highest emergence.

There was a significant interaction effect between seed mix richness and precipitation treatment on sown species emergence ($\chi^2_{(2,83)}$ =7.97, p=0.02, **Figure 2.5b**). The high richness mix led to slightly higher emergence of sown species under low and mean precipitation treatments; however, emergence was significantly lower for the high richness mix under the high precipitation treatment. There was not a significant interaction between seed mix richness and year in the rain-out plots ($\chi^2_{(2,83)}$ =2.55, p=0.28), nor was there a main effect of mix richness on sown species emergence ($\chi^2_{(1,83)}$ =0.18, p=0.67). Full statistical results for the above are presented in **Table 2.5**.

Community composition varied across three planting years with precipitation held constant $(F_{(2,53)}=5.5, p<0.0001, Figure 2.6)$, again because species varied in their emergence and abundance in different planting years (see Species Responses below). However, composition did not differ under the

three precipitation treatments ($F_{(2,53)}$ =1.3, p=0.10) when *P. capillare* was excluded from analysis. When *P. capillare* was included in the analysis, the three precipitation treatments had different first-year communities as well ($F_{(2,53)}$ =2.4, p=0.007).

Species responses

The three most abundant species in this experiment were *Panicum capillare* (Witchgrass, 1805 seedlings; significant effect of planting year, $\chi^2_{(2,83)}$ =342.67, *p*<0.0001; precipitation treatment, $\chi^2_{(2,83)}$ =27.3, *p*<0.0001; and interaction $\chi^2_{(4,83)}$ =72.63, *p*<0.0001), *Digitaria ischaemum* (Smooth crab grass, 188 seedlings; significant effect of planting year, $\chi^2_{(2,83)}$ =342.67, *p*<0.0001; precipitation treatment, $\chi^2_{(2,83)}$ =27.3, *p*<0.0001), and *Centaurea stoebe* (Spotted knapweed, 186 seedlings, significant effect of planting year, $\chi^2_{(2,83)}$ =8.45, *p*=0.015; no effect of precipitation treatment, $\chi^2_{(2,83)}$ =3.16, *p*=0.21; and significant interaction $\chi^2_{(4,83)}$ =32.13, *p*<0.0001). The three most abundant sown species were *Bouteloua curtipendula* (Side-oats grama, 122 seedlings, significant effect of planting year, $\chi^2_{(2,83)}$ =41.56, *p*<0.0001; precipitation treatment, $\chi^2_{(2,83)}$ =7.30, *p*=0.026), *Echinacea purpurea* (Purple coneflower, 86 seedlings, significant effect of planting year, $\chi^2_{(2,83)}$ =9.33, *p*<0.0001; precipitation treatment, $\chi^2_{(2,83)}$ =8.61, *p*=0.014; no effect of precipitation treatment, $\chi^2_{(2,83)}$ =1.73, *p*=0.42; and no interaction $\chi^2_{(4,83)}$ =2.97, *p*=0.56). These species showed markedly variable responses to planting conditions (**Figure 2.7**). For instance, *E. purpurea* had 8.5 times higher emergence in 2015 than in 2014; while *D. purpurea* had 2.9 times higher emergence in 2015 than in 2014; while *D. purpurea* had 2.9

There was an increase in emergence for these three sown species with decreasing seed mix richness; likely a reflection of the 50% decrease in seeding density for each individual species in the higher diversity mix. *E. purpurea* emerged 1.8 times more in low richness than high richness plots $(\chi^2_{(1,83)}=4.30, p=0.038), D.$ purpurea emerged 2.9 times more in low richness plots $(\chi^2_{(1,83)}=11.14,$

p=0.00084), and *B. curtipendula* emerged 1.4 times more, though this increase was not statistically significant ($\chi^2_{(1,83)}=2.17$, *p*=0.14).

DISCUSSION

Because of the extensive suite of variables controlled, this study provides experimental evidence for year effects during restoration, driven by planting condition effects on seedling emergence. By conducting this experiment within a single site and with identical management techniques, we were able to isolate the effects of planting year and infer a causal relationship between planting conditions and seedling establishment (Vaughn & Young 2010). Along with Stuble et al. (2017), who recently documented year effects in California grasslands in an experiment replicated across years and sites, our results are among the first to document year effects independently of otherwise confounding influences of site and management variation.

Additionally, our precipitation experiment allowed us to directly confront the leading putative hypothesis for year effects: rainfall in the planting year (Bakker et al. 2003; MacDougall et al. 2008). By replicating our precipitation manipulations in each of the three planting years, we were able to disentangle precipitation effects from a suite of other planting conditions that may have varied among years. We found that both sown and non-sown species emerged more with increased water availability, showing that precipitation can cause year effects. However, we also found that sown species emergence varied across years *within* precipitation treatments, meaning non-precipitation factors can also be important drivers of year effects. Future work might evaluate the roles of non-precipitation factors, such as temperature, consumer pressure, pathogen loads, and others to further mechanistic understanding of the causes of year effects. Understanding these drivers will help managers take appropriate rectifying measures; for instance, if temperature prohibits seeds from breaking dormancy in the first growing
season, practitioners may use plugs or simply wait for future seasons; but if consumers and pathogens destroy seeds after sowing, inter-seeding will be necessary for a successful restoration.

We observed substantial variation in the responses of individual species among years and treatments in our experiment. For instance, we found that 2015 was the most conducive year for emergence of sown prairie species, even with precipitation held constant across the years. This pattern is largely driven by the increased emergence of Echinacea purpurea (mean 1.3 out of 4.2 emerged individuals/300 cm² plot) and *Bouteloua curtipendula* (mean 1.6) that year. There was congruence of many conditions that promoted germination for those species. For example, although 2015 was, on average, the coolest year of the three, it was the only year to have 5+ consecutive days in May-June that reached a high of 23.8 C (75°F), which has been shown to be an important germination requirement for E. purpurea (Hassell et al. 2004a; Hassell et al. 2004b). Other species exhibited variable patterns, with some emerging in two (e.g. Coreopsis lanceolata in 2014 and 2016, Oenothera biennis in 2015 and 2016) or one (e.g. Astragalus canadensis in 2014) of the three planting years. Across precipitation treatments, species patterns were far less variable, with only one otherwise present sown species completely absent from drought plots (O. biennis) and most showing increases in emergence rates with increased water, suggesting that it is environmental attributes besides rainfall varying between years that drove many species-level patterns. This variation in responses between species results in a different first-year community composition after different first-year planting conditions. It is this initial community composition upon which all future assembly must build. Without these early community differences, historically contingent community assembly is not possible (Fukami 2015). The first year community assemblage may facilitate, inhibit, or merely tolerate future community members (Connell & Slatyer 1977) and future work will be required to understand the consequences of our emergence results on community assembly.

There was no evidence that increasing seed mix richness improved establishment of sown species in one growing season across planting conditions. We found an interaction between seed mix richness and planting year in ambient (but not rain-out) plots, and an interaction between seed mix richness and precipitation treatment in rain-out plots. Increased seed mix richness did not consistently improve establishment in the first year of restoration. These patterns likely again reflect the variable responses to planting conditions across species, and suggest that including a higher abundance of reliable species (i.e., species that emerge under a wide range of conditions, such as *Dalea purpurea*) can be as valuable to managers as diversifying across species with different emergence requirements when the goal is to improve emergence rates of sown species.

Prairie restoration practitioners have long known the importance of site preparation and weed suppression for restoration success (Rowe 2010), and our results emphasize the ability of weeds to establish at higher rates under wet conditions. Additional mowing prior to seed set should reduce the propagule pressure of weeds after planting, especially in wet years. Watering, although usually logistically infeasible, could improve sown species emergence, but at the cost of increased non-sown emergence. Finally, at a constant seeding rate, including a higher species richness in a seed mix can come at the cost of reducing the abundance of well-performing species (e.g., *D. purpurea, E. purpurea*) and therefore reduce overall initial establishment at a site. Managers should therefore consider this balance between increasing sown species (to increase probability of sown species establishment) when deciding how to allocate resources to their seed mixes (see also Packard & Mutel 1997 for discussion of seed mix design for prairie restoration).

Ecological restoration can be an important tool for promoting biodiversity, but outcomes can vary. Our study shows how planting year conditions can be important in an establishing community. Future work will build on these first-year findings to see whether planting year differences persist over

years to influence community assembly. Lasting year effects will likely vary by species (Werner et al. 2016), and in some cases, first-year communities may leave their mark on communities assembling into the future due to processes of historically contingent assembly (e.g. Lockwood and Samuels 2004, Fukami 2015). In the end, it will be important to examine how year effects matter alongside other major causes of variation in restored communities, e.g. soil edaphic conditions (Grman & Brudvig 2014) and fire frequency (Bowles & Jones 2013).

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APPENDIX

APPENDIX

Figures



Figure 2.1. Methods schematic. Six large plots were restored in each of three study years. Each large plot contained four precipitation treatments: ambient conditions (no rain-out shelter), low precipitation, mean precipitation, or high precipitation. Each precipitation treatment plot contained a high (30 species) and low (8 species) sown richness split plot. Finally, each split-plot contained three randomly distributed sub-sample plots in which seedling emergence and death were monitored.



Figure 2.2. Mean seedling emergence across three planting years for sown and non-sown species under ambient conditions. Mean values are per three pooled 10 x 10-cm sub-sample plots; a total area of 300 cm². All error bars indicate ±1 SE. Letters represent Tukey post-hoc differences within each species group (sown, non-sown) and are corrected for multiple comparisons.



Figure 2.3. Mean seedling emergence across three precipitation treatments for sown and non-sown

species. Mean values are per three pooled 10 x 10-cm sub-sample plots; a total area of 300 cm². All error bars indicate ±1 SE. Letters represent Tukey post-hoc differences within each species group (sown, non-sown) and are corrected for multiple comparisons.



Figure 2.4. Mean seedling emergence across three planting years when precipitation was held constant for (A) sown and (B) non-sown species. Mean values are per three pooled 10 x 10-cm subsample plots; a total area of 300 cm². All error bars indicate ±1 SE. Letters represent Tukey post-hoc differences for planting year within each precipitation treatment and are corrected for multiple comparisons.



Figure 2.5. (A) Interaction between sown richness and planting year on sown species emergence under ambient conditions. (B) Interaction between sown richness and precipitation treatment on sown species emergence. Mean values are per three pooled 10 x 10-cm sub-sample plots; a total area of 300 cm². All error bars indicate ±1 SE. Letters represent Tukey post-hoc differences for planting year within each precipitation treatment and are corrected for multiple comparisons.



Figure 2.6. **Nonmetric multidimensional scaling (NMDS) in three dimensions** (stress=0.19) with Bray-Curtis dissimilarity to visualize differences in plant communities among three planting years (2014, 2015, 2016; R²=0.18) and three precipitation treatments (low, mean, high; R²=0.04) held constant across the years. Ellipses are 95% confidence intervals.



Figure 2.7. Seedling emergence across three planting years and precipitation treatments for the three most abundant non-sown (*Panicum capillare, Digitaria ischaemum,* and *Centaurea stoebe*) and three most abundant sown (*Bouteloua curtipendula, Echinacea purpurea,* and *Dalea purpurea*) species. Because *E. purpurea* was mistakenly replaced with *E. pallida* in 2016, results are not shown *for E. purpurea* in that year. Mean values are per three pooled 10 x 10-cm sub-sample plots; a total area of 300 cm². All error bars indicate ±1 SE. Photos by John Hilty, Illinois Wildflowers.



Figure 2.8. Rain-out shelter design. Rain-out shelters consisted of a clear vinyl roof, t-posts, and a gutter that directed water into a kiddie pool for use in the watering treatments. Each sampled area under the shelter was surrounded by rubber gardening edging to prevent overland flow of water. Numbers near each corner denote the approximate height at that location

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Tables

Table 2.1. Low richness and high richness seed mixes sown. Seed mixes were updated each planting year with fresh seeds from Native Connections (Three Rivers, MI) with updated % pure live seed measurements. During sowing, first each large area was sown with the low diversity mix at a rate of 378.9 seeds/m² (35.2 seeds/ft²) divided evenly among the 8 species in the low richness mix (47.4 seeds/m² each). Then, low richness experimental plots were sown with an additional 378.9 seeds/m² divided evenly among the 8 species (for a total of 94.7 seeds/m² each); while high richness plots were sown with 378.9 seeds/m² divided evenly among 22 different species (17.2 seeds/m² each).

Seed mixes sown (seeding rate in seeds/m ²)								
Species name	Common name	Туре	Low	High				
Andropogon gerardii	Big Bluestem	C4 grass	94.7	47.4				
Bouteloua curtipendula	Side Oats Grama	C4 grass	94.7	47.4				
Bromus kalmii	Prairie Brome	C3 Grass		17.2				
Calamagrostis canadensis	Bluejoint Grass	C3 Grass		17.2				
Elymus canadensis	Canada Wild Rye	C3 Grass	94.7	47.4				
Koeleria macrantha	Junegrass	C3 Grass		17.2				
Panicum virgatum	Switchgrass	C4 grass		17.2				
Schizachyrium scoparium	Little Bluestem	C4 grass		17.2				
Sorghastrum nutans	Indian Grass	C4 grass		17.2				
Asclepias tuberosa	Butterflyweed	Forb		17.2				
Astragalus canadensis	Canadian Milkvetch	Legume		17.2				
Baptisia alba	White Wild Indigo	Legume		17.2				
Chamaechrista fasciculata	Partridge Pea	Legume	94.7	47.4				
Coreopsis lanceolata	Lance-leaf Coreopsis	Forb		17.2				
Dalea purpurea	Purple Prairie Clover	Legume	94.7	47.4				

Table 2.1 (cont'd)

Desmodium canadense	Showy Tick Trefoil	Legume	—	17.2
Echinacea purpurea/pallida	Purple/Pale Coneflower	Forb	94.7	47.4
Eryngium yuccifolium	Rattlesnake Master	Forb	94.7	47.4
Heliopsis helianthoides	False Sunflower	Forb		17.2
Oenothera biennis	Evening Primrose	Forb	—	17.2
Oligoneuron rigidum	Stiff Goldenrod	Forb	—	17.2
Penstemon digitalis	Foxglove Beardtongue	Forb	94.7	47.4
Potentilla arguta	Prairie Cinquefoil	Forb	—	17.2
Ratibida pinnata	Gray-headed Coneflower	Forb	—	17.2
Rudbeckia hirta	Black-eyed Susan	Forb		17.2
Scrophularia lanceolata	Lanceleaf Figwort	Forb		17.2
Symphyotrichum urophyllum	Arrow-leaf Aster	Forb	—	17.2
Tephrosia virginiana	Goat's Rue	Legume		17.2
Verbena stricta	Hoary Vervain	Forb		17.2
Verbesina alternifolia	Wingstem	Forb		17.2
		Total	757.8	757.8

Table 2.2. Overview of results with Panicum capillare included. ⁺Denotes result's significance is

different when *P. capillare* excluded.

Predictor	χ ²	df	p-value	Post-hoc contrasts				
Non-sown seedling emergence in ambient conditions								
				2014-2015, z=-8.3, p<0.0001***				
Planting year	167.1	2, 28	<0.0001***	2014-2016, z=-12.7, p<0.0001***†				
				2015-2016, z=5.6, p<0.0001***				
Non-sown seedling death in ambient conditions								
Planting year	2.0	2, 28	0.37†	NA [†]				
Non-sown seedling ei	mergence	in wate	ring treatments					
				2014-2015, z=-9.1, p<0.0001***†				
Planting year	288.8	2, 84	<0.0001***†	2014-2016, z=-15.2, p<0.0001***†				
				2015-2016, z=-6.3, p<0.0001***†				
				low-mean: z=-3.5, p=0.002**				
Watering treatment	42.7	2, 84	<0.0001***	low-high: z=5.9, p<0.001***				
				mean-high: z=2.5, p=0.04+				
Year * watering	108.8	4, 84	<0.0001***	NA				
Non-sown seedling survival in watering treatments								
				2014-2015: z=5.2, p<0.0001***				
Planting year	30.1	2, 80	<0.0001***	2014-2016: z=0.4, p=0.91				
				2015-2016: z=-5.3, p<0.0001***†				
Watering treatment	2.2	2, 80	0.33	NA				
First year plant comm	nunity in a	mbient	conditions					
Diantinguage	F=1.9	2 17	0.04*					
Planting year	R ² =0.20	2,17	0.04*	NA				
First year plant community in watering treatments								
Dianting year	F=6.9	2 52	<0.0001***	NA				
Planting year	R ² =0.20	2, 55	<0.0001	NA				
Watering treatment	F=2.4	2 52	0 007**+	NA				
	R ² =0.07	2, 53	0.007	NA				
Voor * wotoring	F=1.0	4 52	0.22	NA				
real watering	R ² =0.06	4, 53	0.32	INA				

Table 2.3. Plot-level means for seedling survival measured across three planting years in ambient andwatering treatment plots. "All species" category includes sown, non-sown, and unknown species. Meanvalues (n=6) are per 3 pooled 10 cm x 10 cm sub-sample plots; a total area of 0.03 m².

Ambient & rain-out p Plot level means	2014	2015	2016		
		Sown	0.2	0.0	0.3
	Mean # died	Non-sown	0.2	0.3	0.9
Ambient Plots		All	0.7	0.8	2.4
(no rain-out shelter)		Sown	94.9%	100.0%	93.5%
	% Survived	Non-sown	97.8%	98.9%	97.4%
		All	96.1%	97.8%	94.2%
		Sown	0.0	0.4	0.0
	Mean # died	Non-sown	0.3	0.0	0.8
Treatment 1		All	0.3	0.3	1.2
(low precipitation)		Sown	100.0%	79.5%	100.0%
	% Survived	Non-sown	96.4%	100.0%	92.8%
		All	96.4%	97.6%	91.4%
		Sown	0.0	0.0	0.3
	Mean # died	Non-sown	0.3	0.0	2.2
Treatment 2		All	0.9	0.3	2.8
(mean precipitation)		Sown	100.0%	100.0%	89.3%
	% Survived	Non-sown	97.1%	100.0%	93.6%
		All	94.6%	98.9%	93.1%
Treatment 3		Sown	0.1	0.2	0.3
	Mean # died	Non-sown	1.4	0.5	2.1
		All	2.0	0.9	3.5
(high precipitation)		Sown	95.5%	96.9%	92.0%
	% Survived	Non-sown	87.5%	98.8%	94.3%
		All	87.7%	98.1%	92.1%

Table 2.4. Statistical results for planting restored prairie in three planting years (ambient conditions).

Post hoc tests on statistically significant main effects (α =0.05) used Tukey contrasts. †Result *p*>0.05 or ††result *p*<0.05 when *P. capillare* included, see **Table 2.2.**

A. Seedling emergence in ambient conditions								
Predictor	χ^2	df	p-value	Post hoc contrasts				
Sown species								
Planting year	37.4	2, 25	<0.0001***	2014-2015, <i>z</i> =-5.8, <i>p</i> <0.0001***				
(See Figure 2a)				2014-2016, <i>z</i> =-1.4, <i>p</i> =0.35 ⁺⁺				
				2015-2016, <i>z</i> =4.5, <i>p</i> <0.0001***				
Seed mix richness	3.5	1, 25	0.06	NA				
Year * richness	6.4	2, 25	0.04*	Year effect dependent on richness:				
(See Figure 5a)				High mix richness:				
				2014-2015, z=-4.82, p<0.0001***				
				2014-2016, z=-2.87, p=0.011*				
				2015-2016, z=2.27, p=0.060				
				Low mix richness:				
				2014-2015, z=-3.35, p=0.0024**				
				2014-2016, z=0.76, p=0.73				
				2015-2016, z=3.96, p=0.0002***				
				Richness effect dependent on year:				
				2014, z=-0.76, p=0.45				
				2015, z=1.04, p=0.30				
				2016, <i>z</i> =2.87, <i>p</i> =0.0041**				
Non-sown species								
Planting year	37.5	2, 28	<0.0001***	2014-2015, <i>z</i> =-4.5, <i>p</i> <0.0001***				
(See Figure 2b)				2014-2016, <i>z</i> =1.0, <i>p</i> =0.55				
				2015-2016, <i>z</i> =5.4, <i>p</i> <0.0001***				
B. Seedling death i	n ambi	ent con	ditions					
Predictor	χ^2	df	p-value	contrasts				
Sown species								
NA— of 168 seedlings in ambient plots, only 5 died								
Non-sown species								
Planting year	20.7	2, 28	<0.0001***†	2014-2015, <i>z</i> =0.67, <i>p</i> =0.78				
				2014-2016, z=-3.2, p=0.004**†				
				2015-2016, z=-4.1, p=0.0001***†				

Table 2.5. Statistical results for planting restored prairie with three watering treatments in three

planting years. Tukey contrast *p*-values adjusted for comparing families of three estimates. *†*Result

p>0.05 or ++result p<0.05 when P. capillare included, see **Table 2.2**.

A. Seedling emergence in watering treatments					
Predictor	χ^2	df	p-value	Post hoc contrasts	
Sown species					
Planting year	51.9	2, 83	<0.0001***	2014-2015: <i>z</i> =-5.7, <i>p</i> <0.0001***	
				2014-2016: <i>z</i> =-1.3, <i>p</i> =0.40	
				2015-2016: <i>z</i> =4.5, <i>p</i> <0.0001***	
Watering treatment	25.6	2, 83	<0.0001***	low-mean: z=-3.6, p=0.001**	
				low-high: <i>z</i> =4.7, <i>p</i> <0.0001***	
				mean-high: <i>z</i> =1.2, <i>p</i> =0.47	
Seed mix richness	0.18	1, 83	0.67	NA	
Year * watering	3.21	4, 83	0.52	NA	
Year * richness	2.55	2, 83	0.28	NA	
Watering * richness	7.97	2, 83	0.02*	Watering effect dependent on richness:	
(See figure 5b)				Low richness: low-mean, z=-3.12, p=0.0052**	
				low-high, z=5.07, p<0.001**	
				mean-high, <i>z</i> =2.25, <i>p</i> =0.064	
				High richness: low-mean, z=-2.64, p=0.023*	
				low-high, z=2.41, p=0.043*	
				mean-high, z=-0.24, p=0.97	
				Richness effect dependent on watering:	
				low, <i>z</i> =1.20, <i>p</i> =0.23	
				mean, <i>z</i> =0.67, <i>p</i> =0.51	
				high, z=-2.52, p=0.012*	

Non-sown species				
Planting year	5.39	2, 84	0.07†	NA
Watering treatment	19.0	2, 84	<0.0001***	low-mean: z=-3.0, p=0.009**
				low-high: <i>z</i> =5.1 <i>, p</i> <0.001***
				mean-high: <i>z</i> =2.2, <i>p</i> =0.07++
Year * watering	39.4	4, 84	<0.0001***	Year effect dependent on watering:
(See figure 5c)				Low: 2014-2015, <i>z</i> =4.24, <i>p</i> =0.0001***
				2014-2016, <i>z</i> =4.87, <i>p</i> <0.0001***
				2015-2016, <i>z</i> =0.84, <i>p</i> =0.68
				Mean: 2014-2015, <i>z</i> =1.15, <i>p</i> =0.48
				2014-2016, <i>z</i> =0.00, <i>p</i> =1.00
				2015-2016, z=-1.15, p=0.48
				High: 2014-2015, <i>z</i> =-2.66, <i>p</i> =0.022*
				2014-2016, <i>z</i> =0.00, <i>p</i> =1.00
				2015-2016, <i>z</i> =2.66, <i>p</i> =0.022*
				Watering effect dependent on year:
				2014: low-mean, z=-0.59, p=0.83
				low-high, z=1.96, p=0.11
				mean-high, <i>z</i> =1.39, <i>p</i> =0.35
				2015: low-mean, z=-2.76, p=0.016*
				low-high, z=5.73, p<0.0001***
				mean-high <i>, z</i> =3.22 <i>, p</i> =0.0037**
				2016: low-mean, z=-3.92, p=0.0003***
				low-high, z=5.16, p<0.0001***
				mean-high, <i>z</i> =1.39, <i>p</i> =0.35
B. Seedling survival ir	n water	ing trea	atments	

Table 2.5 (cont'd)

B. Seedling survival in watering treatments						
Predictor	χ^2	df	p-value	contrasts		
Sown species						
Planting year	1.85	2, 80	0.40	NA		
Watering treatment	1.17	2, 80	0.56	NA		
Non-sown species						
Planting year	12.6	2, 80	0.002**	2014-2015: <i>z</i> =-3.3, <i>p</i> =0.003**		
				2014-2016: <i>z</i> =-2.0, <i>p</i> =0.11		
				2015-2016: <i>z</i> =0.89, <i>p</i> =0.65++		
Watering treatment	5.91	2, 80	0.05	NA		

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CHAPTER THREE

EXPERIMENTAL MANIPULATION OF PLANTING YEAR CONDITIONS ALTERS PRAIRIE RESTORATION TRAJECTORIES

ABSTRACT

Variation in outcomes of ecological restoration projects is commonplace, and often these outcomes do not match practitioners' goals. This mismatch can suggest a gap in our ecological knowledge of how communities assemble: if we cannot successfully rebuild a community, we have yet to learn something about its assembly. A better understanding of how restored ecological communities assemble will thus inform both ecology and restoration. Interannual variation in environmental conditions at the outset of restoration projects, or "year effects," may contribute to variation among restoration outcomes. However, a lack of experimental tests limits understanding of the mechanisms driving year effects and if these effects persist over time. We conducted an experiment to evaluate year effects on the assembly of plant communities in tallgrass prairie restorations, testing a leading putative mechanism: variation in first year rainfall. We established replicate restored prairie plots at the same site in SW Michigan using identical methods in three different years. During each planting year, we manipulated precipitation with rain-out shelters, and tracked community assembly trajectories for up to four years. We asked how plant community assembly varied across: (i) planting years, (ii) first year precipitation treatments, and (iii) planting years within precipitation treatments (i.e. non-precipitation planting year effects). We also investigated whether the richness of the restoration seed mix used to restore these prairies interacted with planting year conditions to influence assembly trajectories. We found strong evidence that planting years, even when watering was held constant, resulted in different community compositions that lasted into future years. One planting year resulted in significantly higher

cover of non-sown species, while sown species cover and richness fluctuated with each survey year, and the richness of non-sown species was stable across planting years, survey years, and watering treatments. We found no evidence that more diverse seed mixes mitigated any of these year effects. Our results illustrate that planting year effects can vary, demonstrating a complex interplay of deterministic and historically contingent assembly mechanisms, depending on the context. Embracing this unpredictability in restoration outcomes suggests increased focus on post-planting adaptive management that can mediate initial differences in community composition that are not consistent with restoration goals.

INTRODUCTION

Ecological restoration has the potential to slow or reverse biodiversity losses globally (Dobson et al. 1997; Hobbs & Harris 2001; Ruiz-Jaen & Mitchell Aide 2005). However, restoration efforts are prone to unpredictable outcomes, which can be an impediment to their success (Suding 2011; Jones et al. 2018). Understanding why this variation occurs is an important question for restoration research and practice, while also serving as a valuable framework for testing community assembly theories within restored ecosystems (Palmer et al. 1997; Young et al. 2001; Wainwright et al. 2018).

Restoration ecology has traditionally adopted a deterministic view of community assembly, demonstrated by its common use of the watchmaker analogy: just as an expert watchmaker can assemble a working watch from its components, restorationists should be able to reassemble working ecosystems from their parts (Harper 1987). This analogy suggests that restoration outcomes should be predictable and repeatable, given sufficient knowledge of how the systems work that we are trying to restore. However, community ecology theory acknowledges both deterministic and stochastic (unpredictable) drivers of assembly (e.g., Drake 1990; Belyea 2004; Weiher et al. 2011; Fukami 2015)

and the literature shows increasing support for stochastic assembly mechanisms in restoration (e.g., Wilsey et al. 2014; Vaughn & Young 2015; Werner et al. 2016; Young et al. 2016). For instance, experiments altering the assembly histories of restored prairie sites have shown that the timing of arrival of native and exotic species has significant effects on the resulting communities via priority effects (Dickson et al. 2012; Martin & Wilsey 2012). This suggests that the watchmaker analogy may be inadequate for restoration. Instead, the disassembly and reassembly of an ecosystem may not repeatedly render the same outcome, even when conducted in the same way each time. Although this suggests variation may be inevitable, identifying drivers of stochasticity may help us understand variation in restoration outcomes.

In practice, the causes and consequences of variation in assembly history for restoration outcomes remain largely unexplored. There is evidence that weather conditions can exert a selective force on an establishing community (Bakker et al. 2003; Seabloom et al. 2003; MacDougall et al. 2008; Vaughn & Young 2010; Stuble et al. 2017). Despite being an importance source of stochasticity in restoration, differences in planting year weather, often called "year effects," are not well understood by ecologists because the vast majority of restoration projects and ecological studies are not replicated in multiple years (Johnson 2002; Vaughn & Young 2010). Moreover, when planting year effects have been considered in restoration, it has often taken place by comparing sites planted in different years and locations, confounding planting year effects with site characteristics and/or management approaches; few studies have worked to disentangle these effects (though see Stuble et al. 2017; Groves & Brudvig 2018). Restorations initiated by seed sowing should be particularly sensitive to year effects, because of the way species vary in their requirements for germination (Harper 1977; Baskin & Baskin 1988; Larson et al. 2015). As a result, the subset of species emerging from a sown seed mix (as well as the non-sown weed species emerging from the seed bank) is likely to depend on the weather conditions at the time of

or soon after sowing, and this can result in different initial plant communities (Groves and Brudvig 2018).

Most of the evidence for year effects points to variation in precipitation as a key driving mechanism; however, this has rarely been tested (but see Chapter 2; Groves & Brudvig 2018). Most, if not all, studies documenting year effects show correlations with precipitation in the planting year (Bakker et al. 2003; MacDougall et al. 2008; Stuble et al. 2017), but cannot demonstrate causality. There is also literature documenting a correlation between precipitation variability with outcomes of, for instance, competitive interactions between native and exotic species (e.g., Seabloom et al. 2003). That said, there are countless abiotic and biotic variables that could vary inter-annually and have an impact on plant community assembly; for instance, fluctuations in population sizes of rodents (e.g., Getz and Hofmann 1999) could impact a sown community through post-dispersal seed predation (Hulme & Kollmann 2005; Notman & Villegas 2005) or herbivory (Howe & Brown 1999; MacDougall & Wilson 2007; Howe 2008). Many of these variables might also correlate with patterns of precipitation. Alternatively, aspects of weather besides precipitation, like springtime warming patterns that dictate the phenology of germinating plant species (Forrest & James 2011) could in turn alter the identities of early community members (Wainwright & Cleland 2013). Causal evidence is therefore needed to support the hypothesis that precipitation is the leading cause of year effects.

Creating a compelling case for year effects will require understanding of how differences caused by planting year conditions play out over time in an assembling community. Early differences in a community can have significant impact on future community composition because of the way later arrivers interact with the early community, even when the early community members do not persist (Connell & Slatyer 1977; Belyea & Lancaster 1999). However, if deterministic mechanisms drive assembly, differences in initial community composition may dissipate over time.

If year effects are pervasive, managers may seek preventative actions, for instance by sowing a more diverse seed mix that spans a greater range of germination requirements or contains more species that can germinate under a wide range of conditions. A higher seed mix richness should improve total establishment (Myers & Harms 2009) but also might increase variation possible under diverse conditions (Chase 2003; Grman & Brudvig 2014). Additionally, understanding year effects may allow managers to better inform remedial management, for instance the need to sow additional seeds or intensify weed control after certain planting conditions. At present, however, we know of only one study that has considered whether aspects of management can mitigate the influence of year effects for plant communities undergoing restoration (Deering & Young 2006), and none that consider seed mix richness.

We tested the effects of planting year conditions on community assembly in a tallgrass prairie restoration experiment. We planted replicate prairies using identical methods and experimental treatments, in three planting years and followed the communities over time. In a previous paper (Groves & Brudvig 2018), we report results from the first year following establishment of the restoration and found evidence of planting year effects; we now ask whether these lead to longer-term differences in community composition. We follow the communities over time (1-3 years following establishment) to determine if initial differences in communities planted (I) in different years, (II) under different precipitation regimes, and (III) in different years under the same precipitation regimes (i.e. nonprecipitation year effects) persist over time; and (IV) if seed mix richness at planting mediates these year effects and improves the establishment and cover of more sown native species.

METHODS

Study site and restoration methods

We conducted this experiment at the Lux Arbor Reserve in Prairieville, Michigan; a part of Michigan State University's W. K. Kellogg Biological Station. Prior to restoration, the one-hectare field site contained old field vegetation typical to the area (e.g. dominated by *Bromus inermis, Centaurea steobe,* and other native and exotic weedy perennials) and was mowed as needed to prevent woody encroachment. The site was a mixed-oak savanna before being cleared for cultivation sometime before 1946 and was used as a private air-strip in the 1960s and 1970s before its abandonment sometime before 1980.

Experimental design

We used a randomized complete split-split plot design to test the effects of two seed mixes nested within three precipitation treatments within three planting years (n=6 for each treatment combination). In each of three planting years (2014, 2015, 2016), we randomly converted six of eighteen 15.2 m x 36.6 m blocks from old field to tallgrass prairie. For each planting, in early May, as close to the same calendar date as possible, we prepared and planted the blocks by mowing, spraying herbicide (41% glyphosate, 2.5 L/ha), tilling (15.2 cm depth), hand broadcasting native prairie seeds, and cultipacking. Planting was completed on 19-20 May of each planting year, with each blocks (15.2 x 36.6 m) planted each year, four smaller experimental plots (1.0 x 0.5 m) were randomly assigned one of three precipitation treatments or exposed to ambient weather conditions. Precipitation treatments were controlled with rain-out shelters that diverted and collected all rainfall from the plots; the collected rain water was used to water the plots at a steady rate (twice/week) that reflected (a) the 30-year record

low for the area (1.39 cm/month), (b) the 30-year average rainfall (9.91 cm/mo), or (c) above average rainfall (mean + 1.5 standard deviations, 17.81 cm/mo; **Table 3.1**). The experimental plots were surrounded by rubber gardening edging to prevent the overland flow of water in or out of the watering treatment plots. Additional details for this experimental setup can be found in Groves & Brudvig (2018).

The precipitation treatment plots were split again, with one half (0.5 x 0.5 m) randomly assigned to a high species richness treatment that received seeds of 22 additional species (379 seeds/m²) or a low species richness treatment that received seeds of the same 8 species planted in the background (379 seeds/m²). This created two seed mix richness treatments of 8 or 30 species (total sown density, 758 seeds/m²). Species were chosen to represent a typical restoration planting in our area, as well as to ensure the low and high richness mixes had comparable proportions of seeds from different life-form groups (forb, legume, C3 grass, C4 grass; **Table 2.1**). Seed mixes were adjusted each year to account for annual differences in viability of seed, so that each planting received the same amount of live seed for each species. Seeds were local genotypes acquired from the same seed distributor each year.

In 2016, a seed supplying error resulted in sowing *Echinacea pallida* instead of *E. purpurea*; as a result, the relative abundance (percent cover) of these plants was used as a predictor in statistical analyses and not included in any response variables. Because these two species typically differ in establishment success in restorations (*E. purpurea* is known to establish readily while *E. pallida* is notoriously difficult; this was confirmed in our field studies), we felt this was a fair way to ensure these plants did not confound our results. Additionally, one of the non-sown species prevalent in the first-year community, *Panicum capillare*, set seed again after being mowed to prevent propagule pressure from the planted prairies to affect the neighboring plots. We saw an increase in abundance of this species in each subsequent planting year, and believe this is an artifact of the experimental design, and not a true year effect. Therefore, we have also used the abundance of this species in the planting year as a predictor throughout each statistical model, and excluded it from all response variables.

Plant surveys

We conducted surveys of the plant community in each 0.5 x 0.5 m experimental plot in late July each year (2014-2017) by visually identifying each species and quantifying the percent cover of the plot it occupied.

Statistical analyses

We used linear mixed models to examine how sown and non-sown species richness and cover responded to fixed effects of planting year, seed mix richness, and watering treatment (where relevant), random effects of block and plot the abundance of *Echinacea sp.* and the abundance of *P. capillare* in the planting year (detailed above; package "lme4," Bates et al. 2015). We considered ambient (no rainout shelter) and precipitation treatment (rain-out shelter) plots in separate analyses in case of possible side effects of the shelters, e.g., greenhouse effects. We analyzed the response of community compositions (averaged across split-plots/seed mix richness treatments) to planting year and watering treatment using permutational multivariate analysis of variance stratified by planting block (PERMANOVA, Anderson 2001; package "vegan," Oksanen et al. 2017). For all analyses, we compared plots by age (1st year, 2nd year, 3rd year) and sampling year (2017), to assess their individual effect on variability within the communities. We visualized differences in plant communities using nonmetric multidimensional scaling (NMDS) in three dimensions using Bray-Curtis dissimilarity. Post-hoc comparisons for significant predictors were conducted using Tukey adjustments for multiple comparisons (package "Ismeans," Lenth 2016), except for PERMANOVA post-hoc tests, for which we manually conducted pairwise comparisons. All analyses were conducted in R version 3.3.2 (Fox and Weisberg 2011; Bates et al. 2015; R Core Team 2016).

RESULTS

Of the 30 species sown, we observed a total of 26 as adults within the experimental plots. Over the 4 years of this experiment, we also observed an additional 66 species that were not sown but emerged within the experimental plots. Weather observed during the 2014, 2015, and 2016 planting years is reported in **Table 3.1**.

Community composition

We found evidence for year effects on the composition of the restored prairie communities. Communities in plots that were exposed to ambient conditions, as well as those that received watering treatments, were dissimilar across the three planting years, and these differences remained over time (**Figure 3.1**; photos, **Figure 3.2**). Initial effects of watering treatments on community composition in the first year dissipated over time, and there was not a significant effect of first-year watering treatment on community composition in later years (**Table 3.2**).

Cover of sown species

We found an effect of planting year on the cover of sown species; however, this appeared to be a result of how age related to survey year (**Figure 3.3**). A comparison of prairie plots in their respective third growing seasons showed 3.8 times higher cover in plots planted in 2015 compared to those planted in 2014 (for ambient first-year plots as well as watering treatment plots, **Table 3.3**). However, this is likely an artifact of the different survey years (2017 and 2016, respectively), because the 2016 growing season resulted in low sown cover for all prairie plots, regardless of planting age (mean 6%), while the 2017 growing season resulted in high sown cover for all prairie plots, regardless of age or initial conditions (mean 24%). Additionally, effects of watering treatment, seed mix richness, or

interactions therein on the cover of sown species did not persist into the third growing season (or 2017, **Table 3.3**).

Richness of sown species

The richness of sown prairie species likewise was more dependent on the conditions in the year of the survey than those in the year of planting (**Figure 3.4**). Prairie plots planted in 2014, though they had lower sown species richness in their first year when compared to 2015 and 2016 plots (**Figure 3.4**), no longer had significantly lower richness by 2017 (**Table 3.4**). Although the mean and high watering treatments had significantly higher richness in the first growing season, these effects did not persist into the third growing season (or 2017, **Table 3.4**). Finally, increased seed mix richness did increase the richness of sown species observed across all years; however, we found no significant interactions between seed mix richness and planting year or watering treatment, suggesting that mix richness does not alter the impact of planting year effects.

Non-sown species

Year effects were apparent in the cover of non-sown species, driven by differences in the 2016 prairie plots (**Figure 3.5**). Non-sown cover in the planting year was negatively correlated with the abundance of *P. capillare* (**Table 3.5**). *P. capillare*, an annual, was not present in later growing seasons, and non-sown cover in all plots increased over time (**Figure 3.5**). However, the 2016 plantings, which had the most *P. capillare* and the least cover of all other non-sown species in their first year, had the most non-sown cover of all the prairies in their second year, 2017—especially in plots that had been watered in their first year—and surpassed the steady increase in non-sown cover seen in the 2014 and 2015 plantings. We found a significant effect of planting year on non-sown cover across second year plots and across 2017 plots because of this spike in non-sown cover for these 2016 plots in their second
year. We found no other significant predictors for non-sown cover that persisted into their third growing season (or 2017, **Table 3.5**). We found no effect of planting year, watering treatment, or seed mix richness on the richness of non-sown species during any year after planting (**Table 3.6**).

DISCUSSION

We provide experimental evidence that planting year effects alter community assembly trajectories in restoration. Specifically, we found that after holding all site and management variables constant—even watering the same amount— plant communities differed across planting years and these differences persisted. These differences were not caused by watering, because although the watering treatments resulted in different first-year communities, these differences did not persist over time. Instead, these results suggest that a factor besides water availability drive year effects on these communities. Additionally, although high seed mix richness increased the richness of sown species, we found no evidence that that increased richness mitigated planting year effects to improve establishment and cover of sown native species. Finally, we found that key metrics of restoration success, namely sown and non-sown cover and sown and non-sown species richness, were generally not affected by year effects. Sown cover and sown richness both varied in tandem with favorable and unfavorable growing seasons, regardless of their planting year, and non-sown richness showed no response to planting year, survey year, or watering treatment. Only the cover of non-sown species was different across plots planted in different years, with the 2016 plantings having significantly higher weed cover in their second year than any other plantings then or in any prior year.

Our direct test of planting year, along with manipulation of precipitation— the leading hypothesized mechanism for planting year effects— allows us to infer causality for these effects without confounding with site- and management-related variables. We did not find evidence that precipitation

caused year effects; on the contrary, we found that year-to-year variation was important even across plots where precipitation had been held constant in different years. This mechanistic backing suggests that some other factor—likely correlated with precipitation—may have been at play in previous studies that have documented year effects that correlated with rainfall (Bakker et al. 2003; MacDougall et al. 2008; Vaughn & Young 2010; Stuble et al. 2017).

The planting-year differences we saw in community composition persisted into later growing seasons. This is an important consideration, given that under deterministic assembly, communities could converge in response to weather or other conditions (e.g. soils) in later years despite initial differences (e.g., Weiher et al. 1998; Turnbull et al. 2005). Tracking these communities over time allowed us to disentangle planting year effects from effects of survey years and site age (Stuble et al. 2017). Further monitoring of this site will allow us to evaluate whether or not these communities will eventually converge and, if so, over what time scale.

The plantings that resulted in the most non-sown species cover were planted in the year with the driest summer (2016, **Table 3.1**). Other studies documenting year effects have demonstrated similar patterns, e.g. Bakker et al. (2003) and MacDougall et al. (2008) saw a strong hinderance to restoration outcomes after a particularly dry planting year, while two other normal planting years had similar outcomes to one another. Because we also manipulated rainfall availability directly through watering each year, and found no effect on non-sown species cover, we can infer that it is not the lack of rainfall alone that causes these differences in assembly in these restored communities. Instead, there may be other factors that correlate with a dry summer—such as variation in heat, humidity, or cloud cover—that influence the phenology of the sown and non-sown seeds, or that biotic considerations like granivores and herbivores are at play (e.g., Hulme & Kollmann 2005; Howe 2008; Wainwright & Cleland 2013). More research is needed to disentangle the influence, and relative impact, of these drivers.

Increased seed mix richness was correlated with increased sown species richness across our experiment. Increasing mix richness has many proven benefits in restoration (e.g. Nemec et al. 2013; reviewed in Myers & Harms 2009). We did not, however, find evidence that increasing mix richness mitigated planting year effects (see also Carter & Blair 2012). We predicted to find interactions between mix richness and planting year conditions, driven by an increased likelihood that the high richness mix would contain species suited for any given conditions (Chase 2003; Tilman et al. 2006). We found no such interactions except one transient (i.e. seen in 2nd-year prairies only) in which the low richness seed mix correlated with an increase in relative abundance of sown species for prairies planted in 2016. Instead of seeing the "portfolio effects" (Hooper 2005; Schindler et al. 2015) that we expected, in which diversity decreases risk of establishment failure and increases total success, this seemingly counterintuitive result highlights the potential that a less diverse mix, though theoretically riskier, will occasionally be particularly suited for the conditions and out-perform the high richness mix in terms of total establishment (e.g., Aarssen et al. 2003). This outcome might be particularly common in restoration, where less diverse seed mixes are typically compositional subsets of the most reliable species found in more diverse seed mixes (e.g., Packard & Mutel 1997; see Groves & Brudvig 2018). When this is the case, post-first-year management may be necessary to mitigate year effects. For instance, additional seed additions or increased weed control following for restorations planted during poor conditions may be very important (Rowe 2010; Wilson 2015).

One possible unintended source of variation in this experiment is the introduction of year effects through the seed mix. Our seeds were sourced from the same supplier each year and adjusted based on annually updated tests of seed viability; however, these seed "populations" could have been genetically distinct across years in a way that impacted how they would respond to the site or weather conditions. Seeds collected in different years could also come from maternal plants that have faced

different conditions as they produced seed, leading to different seed quality between batches, regardless of general viability (Roach & Wulff 1987; Mousseau & Fox 1998; Wang & Frei 2011).

Our work highlights the important role of stochasticity in community assembly. Strong effects of planting conditions on community composition in the first year persisted into subsequent growing seasons. However, basic metrics of restoration success often responded more to weather or other conditions in later survey years. We sought to make broad generalizations about assembly trajectories in this system by controlling as many factors as possible (site, management, and sown species), and the data tell a compelling story about variation in composition across similarly "good" outcomes. Returning to the watch maker analogy, we learned that ensuring that watch parts are the same does not ensure recreation of the same watch; quite the contrary—restoration trajectories are diverse in ways that remain unexplained. This variation can be a good thing, as long as it stays within the bounds of what we'd consider acceptable outcomes for restoration. In other words, we don't want to increase variation among outcomes by including failures, but variation in general can increase beta diversity across sites and, thus, landscape-level diversity. Managers working in restoration may benefit from expecting and embracing this variation, sharing their attention between trusted restoration methods and how to respond to divergent outcomes from those same methods.

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APPENDIX

Figures



Figure 3.1. Non-metric Multidimensional Scaling (NMDS) of plots planted in 2014, 2015, and 2016 over time. Plots shown received watering treatments in their first growing season. (A) shows the progression of individual plots. Points of each color group (red, purple, green) represent plots planted in the three planting years (2014, 2015, 2016, respectively) and become darker with age. (B) shows the centroid of each group of plots. For both, points closer together represent communities that are more similar in their species composition.



Figure 3.2 Photos taken in 2017 of prairie plots planted in (A) 2014, (B) 2015, and (C) 2016. Phots were taken July 25-August 1, 2017, at the W.K. Kellogg Biological Station's Lux Arbor Reserve in Prairieville, Michigan.





first year.



Figure 3.4. Sown species richness over time in plots that were exposed to ambient conditions in their

first year.



Figure 3.5. Non-sown species cover over time in plots that received watering treatments in their first year.

Table 3.1. Weather conditions in three planting years. 1981-2010 averages from Michigan State

Climatologist's Office (Gull Lake Weather Station, https://climate.geo.msu.edu, accessed 14 May 2018).

2014-2016 records from Weather Underground (Battle Creek Weather Station,

https://www.wunderground.com, accessed 14 May 2018).

	Spr (Marc	ing weath ch 1 – Maγ	er / 31)	Sum (Jun	mer weat e 1 – July	her 31)
	Average low temperature (°C)	Average high temperature (°C)	Total precipitation (cm)	Average low temperature (°C)	Average high temperature (°C)	Total precipitation (cm)
1981-2010	2.9	15.8	25.5	15.1	28.5	19.9
2014	1.1	12.8	16.3	15.6	25.6	24.8
2015	3.3	15.0	18.4	15.6	26.1	32.5
2016	3.9	15.0	21.2	15.0	27.2	13.4

averaged across high and low seed mix richness. PERMANOVA models for watered first-year plots are stratified by block. *P. capillare* abundance included as a model predictor refers to the abundance of that species in the planting year. *Echinacea sp.* abundance included as a model predictor refers to abundance of that species in the survey year. Pairwise comparisons were conducted manually using subsetted data in the PERMANOVA models.

Table 3.2. Statistical model results predicting similarity of community composition. Subplots are

A. In plots exposed to ambient weather conditions in their first year						
Community dissimilarity in	the fir	st year				
Predictor	F	p-value	R ²	Model R ² =0.21		
Year planted	2.52	0.0002***	0.13	2014-2015 F=1.66, p=0.093		
				2014-2016 F=2.62, p=0.00030***		
				2015-2016 F=3.12, p=0.00020***		
Echinacea sp. abundance	0.90	0.56	0.023			
P. capillare abundance	2.16	0.0078**	0.055			
Community dissimilarity in	the se	cond year				
Predictor	F	p-value	R ²	Model R ² =0.25		
Year planted	4.21	0.0002***	0.20	2014-2015 F=5.79, p<0.0001***		
				2014-2016 F=4.49, p=0.00020***		
				2015-2016 F=2.41, p=0.020*		
Echinacea sp. abundance	0.52	0.90	0.013			
P. capillare abundance	1.17	0.29	0.028			
Community dissimilarity in	the th	ird year				
Predictor	F	p-value	R ²	Model R ² =0.29		
Year planted	4.03	0.0021**	0.14			
Echinacea sp. abundance	0.61	0.72	0.022			
P. capillare abundance	3.50	0.0035**	0.12			
Community dissimilarity in	2017					
Predictor	F	p-value	R ²	Model R ² =0.25		
Year planted	4.10	<0.0001***	0.20	2014-2015 F=2.85, p=0.0099**		
				2014-2016 F=4.70, p<0.0001***		
				2015-2016 F=4.49, p<0.0001***		
Echinacea sp. abundance	0.62	0.80	0.015			
P. capillare abundance	1.70	0.083	0.041			

Table 3.2 (cont'd)

Community dissimilarity in	Community dissimilarity in the year planted						
Predictor	F	p-value	R ²	Model R ² =0.21			
Year planted	5.33	<0.0001***	0.091	2014-2015 F=5.38, p<0.0001***			
				2014-2016 F=6.86, p<0.0001***			
				2015-2016 F=3.84, p<0.0001***			
Watering treatment	1.56	0.019*	0.027	Low-mean F=1.58, p=0.029*			
				Low-high F=1.58, p=0.024*			
				Mean-high F=1.58, p=0.026*			
Echinacea sp. abundance	1.42	0.12	0.012				
P. capillare abundance	3.34	<0.0001***	0.028				
Year planted * Watering	1.51	0.0040**	0.051				
Community dissimilarity in	n the se	cond year					
Predictor	F	p-value	R^2	Model R ² =0.25			
Year planted	8.22	<0.001***	0.13	2014-2015 F=7.44, p<0.0001***			
				2014-2016 F=7.50, p<0.0001***			
				2015-2016 F=6.70, p<0.0001***			
Watering treatment	1.43	0.069	0.023				
Echinacea sp. abundance	3.26	0.0012**	0.026				
P. capillare abundance	2.06	0.018*	0.017				
Year planted * Watering	1.55	0.0086**	0.050				
Community dissimilarity in	the th	ird year					
Predictor	F	p-value	R^2	Model R ² =0.18			
Year planted	6.56	<0.001***	0.084				
Watering treatment	1.19	0.22	0.030				
Echinacea sp. abundance	1.42	0.35	0.018				
P. capillare abundance	1.28	0.14	0.016				
Year planted * Watering	1.44	0.10	0.037				
Community dissimilarity in	2017						
Predictor	F	p-value	R^2	Model R ² =0.25			
Year planted	9.84	<0.001***	0.16	2014-2015 F=6.15, p<0.0001***			
				2014-2016 F=13.76, p<0.0001***			
				2015-2016 F=6.63, p<0.0001***			
Watering treatment	1.30	0.15	0.021				
Echinacea sp. abundance	1.48	0.15	0.012				
P. capillare abundance	0.71	0.65	0.0056				
Year planted * Watering	1.76	0.0033**	0.056				

B. In plots receiving watering treatments in their first year

Table 3.3. Statistical model results predicting the cover of sown species. Linear mixed effect models for ambient first-year plots included a random effect of plot; models for watered first-year plots included random effects of plot and block. Cover of sown species was log(x+0.05) transformed to improve model fit. *P. capillare* abundance included as a model predictor refers to the abundance of that species in the planting year. *Echinacea sp.* abundance included as a model predictor refers to abundance of that species in the survey year.

A. In plots exposed to amb	ient weat	ther condition	ons in the	ir first year
Cover of sown species in th	e year pl	anted		
Predictor	χ^2	p-value	R ²	Model R ² =0.21
(Intercept)	7.07	0.0079		
Year planted	4.43	0.11	0.098	
Seed mix richness	0.26	0.61	0.0050	
Echinacea sp. abundance	0.24	0.62	0.0070	
P. capillare abundance	0.78	0.38	0.032	
Seed mix * Year planted	0.48	0.79	0.000	
Cover of sown species in th	e second	year		
Predictor	χ^2	p-value	R ²	Model R ² =0.29
(Intercept)	10.94	0.00094		
Year planted	4.21	0.12	0.14	
Seed mix richness	0.38	0.54	0.0070	
Echinacea sp. abundance	0.55	0.46	0.014	
P. capillare abundance	0.53	0.47	0.023	
Seed mix * Year planted	9.80	0.0075**	0.19	
Cover of sown species in th	e third ye	ear		
Predictor	χ ²	p-value	<i>R</i> ²	Model R ² =0.61
(Intercept)	7.29	0.0069		
Year planted	6.80	0.0091**	0.25	
Seed mix richness	2.68	0.10	0.12	
Echinacea sp. abundance	0.0011	0.97	0.00	
P. capillare abundance	4.91	0.027*	0.20	
Seed mix * Year planted	1.16	0.28	0.055	
Cover of sown species in 20	017			
Predictor	χ ²	p-value	<i>R</i> ²	Model R ² =0.33
(Intercept)	24.98	<0.0001		
Year planted	0.46	0.79	0.017	
Seed mix richness	3.60	0.058	0.081	
Echinacea sp. abundance	1.12	0.29	0.034	
P. capillare abundance	1.40	0.24	0.051	
Seed mix * Year planted	3.30	0.19	0.039	

Table 3.3 (cont'd)

Cover of sown species in the year planted									
Predictor	χ^2	p-value	<i>R</i> ²	Model R ² =0.28					
(Intercept)	5.98	0.014							
Year planted	3.24	0.20	0.046						
Watering treatment	2.57	0.28	0.014						
Seed mix richness	0.0052	0.94	0.000						
Echinacea sp. abundance	0.077	0.78	0.0010						
<i>P. capillare</i> abundance	4.76	0.029*	0.043						
Year planted * Watering	12.34	0.015*	0.11						
Seed mix * Year planted	3.51	0.17	0.045						
Seed mix * Watering	0.13	0.94	0.0010						
Cover of sown species in th	ne second	year							
Predictor	χ^2	p-value	R ²	Model R ² =0.33					
(Intercept)	9.33	0.0023							
Year planted	4.30	0.12	0.061						
Watering treatment	4.55	0.10	0.027						
Seed mix richness	6.72	0.010**	0.041						
Echinacea sp. abundance	1.85	0.17	0.018						
P. capillare abundance	0.13	0.72	0.0020						
Year planted * Watering	2.24	0.69	0.037						
Seed mix * Year planted	4.64	0.098	0.041						
Seed mix * Watering	5.97	0.051	0.043						
Cover of sown species in th	ne third ye	ear							
				-					
Predictor	χ^2	p-value	R ²	Model R ² =0.47					
Predictor (Intercept)	<u>χ</u> ² 8.60	<i>p-value</i> 0.0034	R ²	Model R ² =0.47					
Predictor (Intercept) Year planted	χ ² 8.60 3.40	<i>p-value</i> 0.0034 0.065	<i>R</i> ² 0.067	Model R ² =0.47					
Predictor (Intercept) Year planted Watering treatment	χ ² 8.60 3.40 5.24	<i>p-value</i> 0.0034 0.065 0.073	<i>R</i> ² 0.067 0.056	<i>Model R</i> ² =0.47					
Predictor (Intercept) Year planted Watering treatment Seed mix richness	χ ² 8.60 3.40 5.24 2.48	<i>p-value</i> 0.0034 0.065 0.073 0.12	<i>R</i> ² 0.067 0.056 0.020	Model R ² =0.47					
Predictor (Intercept) Year planted Watering treatment Seed mix richness Echinacea sp. abundance	χ ² 8.60 3.40 5.24 2.48 0.94	<i>p-value</i> 0.0034 0.065 0.073 0.12 0.33	<i>R</i> ² 0.067 0.056 0.020 0.014	Model R ² =0.47					
Predictor (Intercept) Year planted Watering treatment Seed mix richness Echinacea sp. abundance P. capillare abundance	χ ² 8.60 3.40 5.24 2.48 0.94 0.67	<i>p-value</i> 0.0034 0.065 0.073 0.12 0.33 0.41	<i>R</i> ² 0.067 0.056 0.020 0.014 0.012	Model R ² =0.47					
Predictor (Intercept) Year planted Watering treatment Seed mix richness Echinacea sp. abundance P. capillare abundance Year planted * Watering	<u>χ</u> ² 8.60 3.40 5.24 2.48 0.94 0.67 1.09	<i>p-value</i> 0.0034 0.065 0.073 0.12 0.33 0.41 0.58	R ² 0.067 0.056 0.020 0.014 0.012 0.014	<i>Model R</i> ² <i>=</i> 0.47					
Predictor (Intercept) Year planted Watering treatment Seed mix richness Echinacea sp. abundance P. capillare abundance Year planted * Watering Seed mix * Year planted	χ ² 8.60 3.40 5.24 2.48 0.94 0.67 1.09 1.33	<i>p-value</i> 0.0034 0.065 0.073 0.12 0.33 0.41 0.58 0.25	R ² 0.067 0.056 0.020 0.014 0.012 0.014 0.012 0.014	Model R ² =0.47					
Predictor (Intercept) Year planted Watering treatment Seed mix richness Echinacea sp. abundance P. capillare abundance Year planted * Watering Seed mix * Year planted Seed mix * Watering	$\frac{\chi^2}{8.60}$ 3.40 5.24 2.48 0.94 0.67 1.09 1.33 0.83	p-value 0.0034 0.065 0.073 0.12 0.33 0.41 0.58 0.25 0.66	R ² 0.067 0.056 0.020 0.014 0.012 0.014 0.012 0.014 0.010 0.0070	Model R ² =0.47					
Predictor (Intercept) Year planted Watering treatment Seed mix richness Echinacea sp. abundance P. capillare abundance Year planted * Watering Seed mix * Year planted Seed mix * Watering Cover of sown species in 20	χ ² 8.60 3.40 5.24 2.48 0.94 0.67 1.09 1.33 0.83 0.7	<i>p-value</i> 0.0034 0.065 0.073 0.12 0.33 0.41 0.58 0.25 0.66	R ² 0.067 0.056 0.020 0.014 0.012 0.014 0.012 0.014 0.010 0.0070	Model R ² =0.47					
Predictor (Intercept) Year planted Watering treatment Seed mix richness Echinacea sp. abundance P. capillare abundance Year planted * Watering Seed mix * Year planted Seed mix * Watering Cover of sown species in 20 Predictor	$\frac{\chi^2}{8.60}$ 3.40 5.24 2.48 0.94 0.67 1.09 1.33 0.83 0.77 χ^2	<i>p-value</i> 0.0034 0.065 0.073 0.12 0.33 0.41 0.58 0.25 0.66 <i>p-value</i>	R ² 0.067 0.056 0.020 0.014 0.012 0.014 0.010 0.0070	<i>Model R²=0.47</i> <i>Model R²=0.32</i>					
Predictor (Intercept) Year planted Watering treatment Seed mix richness Echinacea sp. abundance P. capillare abundance Year planted * Watering Seed mix * Year planted Seed mix * Watering Cover of sown species in 20 Predictor (Intercept)	$\frac{\chi^2}{8.60}$ 3.40 5.24 2.48 0.94 0.67 1.09 1.33 0.83 0.17 χ^2 31.41	p-value 0.0034 0.065 0.073 0.12 0.33 0.41 0.58 0.25 0.66 p-value <0.001	R ² 0.067 0.056 0.020 0.014 0.012 0.014 0.010 0.0070	<i>Model R²=0.47</i> <i>Model R²=0.32</i>					
Predictor(Intercept)Year plantedWatering treatmentSeed mix richnessEchinacea sp. abundanceP. capillare abundanceYear planted * WateringSeed mix * Year plantedSeed mix * WateringCover of sown species in 20Predictor(Intercept)Year planted	$\frac{\chi^2}{8.60}$ 3.40 5.24 2.48 0.94 0.67 1.09 1.33 0.83 017 χ^2 31.41 2.32	p-value 0.0034 0.065 0.073 0.12 0.33 0.41 0.58 0.25 0.66 p-value <0.001	$ \begin{array}{r} R^2 \\ 0.067 \\ 0.056 \\ 0.020 \\ 0.014 \\ 0.012 \\ 0.014 \\ 0.010 \\ 0.0070 \\ R^2 \\ 0.020 \\ \end{array} $	<i>Model R²=0.47</i> <i>Model R²=0.32</i>					
Predictor(Intercept)Year plantedWatering treatmentSeed mix richnessEchinacea sp. abundanceP. capillare abundanceYear planted * WateringSeed mix * Year plantedSeed mix * WateringCover of sown species in 20Predictor(Intercept)Year plantedWatering treatment	$\frac{\chi^2}{8.60}$ 3.40 5.24 2.48 0.94 0.67 1.09 1.33 0.83 017 χ^2 31.41 2.32 3.48	p-value 0.0034 0.065 0.073 0.12 0.33 0.41 0.58 0.25 0.66 p-value <0.001	R^{2} 0.067 0.056 0.020 0.014 0.012 0.014 0.010 0.0070 R^{2} 0.020 0.018	<i>Model R²=0.47</i> <i>Model R²=0.32</i>					
Predictor(Intercept)Year plantedWatering treatmentSeed mix richnessEchinacea sp. abundanceP. capillare abundanceYear planted * WateringSeed mix * Year plantedSeed mix * WateringCover of sown species in 20Predictor(Intercept)Year plantedWatering treatmentSeed mix richness	$\frac{\chi^2}{8.60}$ 3.40 5.24 2.48 0.94 0.67 1.09 1.33 0.83 0.17 χ^2 31.41 2.32 3.48 0.95	p-value 0.0034 0.065 0.073 0.12 0.33 0.41 0.58 0.25 0.66 p-value <0.001	R^{2} 0.067 0.056 0.020 0.014 0.012 0.014 0.010 0.0070 R^{2} 0.020 0.018 0.0070	<i>Model R²=0.47</i> <i>Model R²=0.32</i>					
Predictor(Intercept)Year plantedWatering treatmentSeed mix richnessEchinacea sp. abundanceP. capillare abundanceYear planted * WateringSeed mix * Year plantedSeed mix * WateringCover of sown species in 20Predictor(Intercept)Year plantedWatering treatmentSeed mix richnessEchinacea sp. abundance	$\frac{\chi^2}{8.60}$ 3.40 5.24 2.48 0.94 0.67 1.09 1.33 0.83 017 χ^2 31.41 2.32 3.48 0.95 0.55	p-value 0.0034 0.065 0.073 0.12 0.33 0.41 0.58 0.25 0.66 p-value <0.001	R^{2} 0.067 0.056 0.020 0.014 0.012 0.014 0.010 0.0070 R^{2} 0.020 0.018 0.0070 0.0050	Model R ² =0.47 Model R ² =0.32					
Predictor(Intercept)Year plantedWatering treatmentSeed mix richnessEchinacea sp. abundanceP. capillare abundanceYear planted * WateringSeed mix * Year plantedSeed mix * WateringCover of sown species in 20Predictor(Intercept)Year plantedWatering treatmentSeed mix richnessEchinacea sp. abundanceP. capillare abundance	$\frac{\chi^2}{8.60}$ 3.40 5.24 2.48 0.94 0.67 1.09 1.33 0.83 017 χ^2 31.41 2.32 3.48 0.95 0.55 3.42	p-value 0.0034 0.065 0.073 0.12 0.33 0.41 0.58 0.25 0.66 p-value <0.001	R^{2} 0.067 0.056 0.020 0.014 0.012 0.014 0.010 0.0070 R^{2} 0.020 0.018 0.0070 0.0050 0.037	Model R ² =0.47					
Predictor(Intercept)Year plantedWatering treatmentSeed mix richnessEchinacea sp. abundanceP. capillare abundanceYear planted * WateringSeed mix * Year plantedSeed mix * WateringCover of sown species in 20Predictor(Intercept)Year plantedWatering treatmentSeed mix richnessEchinacea sp. abundanceP. capillare abundanceYear planted	$\frac{\chi^2}{8.60}$ 3.40 5.24 2.48 0.94 0.67 1.09 1.33 0.83 0.17 χ^2 31.41 2.32 3.48 0.95 0.55 3.42 3.03	p-value 0.0034 0.065 0.073 0.12 0.33 0.41 0.58 0.25 0.66 p-value <0.001	R^{2} 0.067 0.056 0.020 0.014 0.012 0.014 0.010 0.0070 R^{2} 0.020 0.018 0.0070 0.0050 0.037 0.026	<i>Model R²=0.47</i> <i>Model R²=0.32</i>					
Predictor(Intercept)Year plantedWatering treatmentSeed mix richnessEchinacea sp. abundanceP. capillare abundanceYear planted * WateringSeed mix * Year plantedSeed mix * WateringCover of sown species in 20Predictor(Intercept)Year plantedWatering treatmentSeed mix richnessEchinacea sp. abundanceP. capillare abundanceYear plantedWatering treatmentSeed mix richnessEchinacea sp. abundanceYear planted * WateringSeed mix * Year planted	$\frac{\chi^2}{8.60}$ 3.40 5.24 2.48 0.94 0.67 1.09 1.33 0.83 0.17 χ^2 31.41 2.32 3.48 0.95 0.55 3.42 3.03 4.09	p-value 0.0034 0.065 0.073 0.12 0.33 0.41 0.58 0.25 0.66 p-value <0.001	R^{2} 0.067 0.056 0.020 0.014 0.012 0.014 0.010 0.0070 R^{2} 0.020 0.018 0.0070 0.0050 0.037 0.026 0.014	Model R ² =0.47					
	Predictor(Intercept)Year plantedWatering treatmentSeed mix richnessEchinacea sp. abundanceP. capillare abundanceYear planted * WateringSeed mix * Year plantedSeed mix * WateringCover of sown species in thePredictor(Intercept)Year plantedWatering treatmentSeed mix richnessEchinacea sp. abundanceP. capillare abundanceYear plantedWatering treatmentSeed mix richnessEchinacea sp. abundanceYear planted * WateringSeed mix * Year plantedSeed mix * Year plantedSeed mix * WateringSeed mix * WateringCover of sown species in the	Predictor χ^2 (Intercept)5.98Year planted3.24Watering treatment2.57Seed mix richness0.0052Echinacea sp. abundance4.76Year planted * Watering12.34Seed mix * Year planted3.51Seed mix * Watering0.13Cover of sown species in the secondPredictorPredictor χ^2 (Intercept)9.33Year planted4.30Watering treatment4.55Seed mix richness6.72Echinacea sp. abundance1.85P. capillare abundance0.13Year planted4.64Seed mix * Year planted4.64Seed mix * Year planted5.97Cover of sown species in the third year	Predictor χ^2 p-value (Intercept) 5.98 0.014 Year planted 3.24 0.20 Watering treatment 2.57 0.28 Seed mix richness 0.0052 0.94 Echinacea sp. abundance 0.077 0.78 P. capillare abundance 4.76 0.029* Year planted * Watering 12.34 0.015* Seed mix * Year planted 3.51 0.17 Seed mix * Watering 0.13 0.94 Cover of sown species in the second year Predictor χ^2 Predictor χ^2 p-value (Intercept) 9.33 0.0023 Year planted 4.30 0.12 Watering treatment 4.55 0.10 Seed mix richness 6.72 0.010** Echinacea sp. abundance 0.13 0.72 Year planted * Watering 2.24 0.69 Seed mix * Year planted 4.64 0.098 Seed mix * Watering 5.97 0.051	Predictor χ^2 p-value R^2 (Intercept)5.980.014Year planted3.240.200.046Watering treatment2.570.280.014Seed mix richness0.00520.940.000Echinacea sp. abundance0.0770.780.0010P. capillare abundance4.760.029*0.043Year planted * Watering12.340.015*0.11Seed mix * Year planted3.510.170.045Seed mix * Watering0.130.940.0010Cover of sown species in the second yearPredictor χ^2 p-valuePredictor χ^2 p-value R^2 (Intercept)9.330.00230.041Watering treatment4.550.100.027Seed mix richness6.720.010**0.041Echinacea sp. abundance1.850.170.018P. capillare abundance0.130.720.0020Year planted * Watering2.240.690.037Seed mix * Year planted4.640.0980.041Seed mix * Year planted4.640.0980.041Seed mix * Watering5.970.0510.043					

B. In plots receiving watering treatments in their first year

Table 3.4. Statistical model results predicting the richness of sown species. Negative binomial mixed effect models for ambient first-year plots included a random effect of plot; models for watered first-year plots included random effects of plot and block. *P. capillare* abundance included as a model predictor refers to the abundance of that species in the planting year. *Echinacea sp.* abundance included as a model predictor refers to abundance of that species in the survey year.

A. In plots exposed to ambient weather conditions in their first year								
Richness of sown species in	Richness of sown species in the year planted							
Predictor	χ^2	p-value	R ²	Model R ² =0.40				
(Intercept)	32.91	<0.001						
Year planted	1.11	0.58	0.027					
Seed mix richness	1.70	0.19	0.067					
Echinacea sp. abundance	3.60	0.058	0.11					
P. capillare abundance	1.14	0.29	0.035					
Seed mix * Year planted	1.47	0.48	0.038					
Richness of sown species in	n the sea	cond year						
Predictor	χ^2	p-value	R ²	Model R ² =0.38				
(Intercept)	27.45	<0.001						
Year planted	3.25	0.20	0.14					
Seed mix richness	0.48	0.49	0.015					
Echinacea sp. abundance	0.17	0.68	0.00					
P. capillare abundance	0.014	0.90	0.001					
Seed mix * Year planted	3.62	0.16	0.14					
Richness of sown species in	n the thi	rd year						
Predictor	χ^2	p-value	R ²	Model R ² =0.45				
(Intercept)	31.32	<0.001						
Year planted	3.86	0.050*	0.20					
Seed mix richness	2.04	0.15	0.10					
Echinacea sp. abundance	0.063	0.80	0.017					
P. capillare abundance	0.73	0.39	0.028					
Seed mix * Year planted	0.54	0.46	0.028					
Richness of sown species in	n 2017							
Predictor	χ^2	p-value	R ²	Model R ² =0.44				
(Intercept)	62.01	<0.001						
Year planted	0.84	0.66	0.045					
Seed mix richness	4.59	0.032	0.10					
Echinacea sp. abundance	0.66	0.42	0.00					
P. capillare abundance	0.10	0.75	0.0020					
Seed mix * Year planted	0.77	0.68	0.042					

Table 3.4 (cont'd)

Richness of sown species in the year planted							
Predictor	χ^2	p-value	R ²	Model R ² =0.62			
(Intercept)	36.19	<0.001					
Year planted	7.58	0.023*	0.16	Tukey post-hoc tests:			
				2014-2015 z=-0.49, p=0.87			
				2014-2016 z=-1.00, p=0.58			
				2015-2016 z=-0.49, p=0.88			
Watering treatment	11.60	0.0030**	0.092	Tukey post-hoc tests:			
				High-low z=3.13, p=0.0049**			
				High-mean z=-0.85, p=0.67			
				Low-mean z=-3.91, p=0.0003**			
Seed mix richness	6.29	0.012*	0.099				
Echinacea sp. abundance	0.089	0.77	0.0010				
P. capillare abundance	0.033	0.86	0.00				
Year planted * Watering	7.53	0.11	0.16				
Seed mix * Year planted	3.64	0.16	0.078				
Seed mix * Watering	0.72	0.70	0.013				
Richness of sown species in	n the sec	ond year					
Predictor	χ^2	p-value	<i>R</i> ²	Model R ² =0.48			
(Intercept)	50.93	<0.0001					
Year planted	2.59	0.27	0.026				
Watering treatment	0.84	0.66	0.010				
Seed mix richness	15.87	<0.0001***	0.17				
Echinacea sp. abundance	3.74	0.053	0.014				
<i>P. capillare</i> abundance	0.19	0.66	0.0020				
Year planted * Watering	0.97	0.91	0.0070				
Seed mix * Year planted	2.00	0.37	0.024				
Seed mix * Watering	4.08	0.13	0.066				
Richness of sown species in	n the thi	rd year					
Predictor	χ^2	p-value	<i>R</i> ²	Model R ² =0.39			
(Intercept)	50.49	<0.0001					
Year planted	0.40	0.53	0.014				
Watering treatment	4.97	0.083	0.050				
Seed mix richness	7.19	0.0073**	0.13				
Echinacea sp. abundance	3.08	0.079	0.031				
P. capillare abundance	0.041	0.84	0.0020				
Year planted * Watering	0.56	0.76	0.021				
Seed mix * Year planted	0.040	0.84	0.00				
Seed mix * Watering	2.46	0.29	0.031				

B. In plots receiving watering treatments in their first year

Table 3.4 (cont'd)

Predictor	χ^2	p-value	R^2	Model R ² =0.46
(Intercept)	30.16	<0.001		
Year planted	3.28	0.19	0.050	
Watering treatment	4.32	0.12	0.032	
Seed mix richness	4.50	0.034*	0.058	
Echinacea sp. abundance	3.90	0.048*	0.033	
P. capillare abundance	0.45	0.50	0.0050	
Year planted * Watering	1.25	0.87	0.029	
Seed mix * Year planted	3.65	0.16	0.048	
Seed mix * Watering	1.04	0.60	0.0070	

Table 3.5. Statistical model results predicting the cover of non-sown species. Linear mixed effect models for ambient first-year plots included a random effect of plot; models for watered first-year plots included random effects of plot and block. Cover of non-sown species was square root transformed to improve model fit. *P. capillare* abundance included as a model predictor refers to the abundance of that species in the planting year. *Echinacea sp.* abundance included as a model predictor refers to abundance of that species in the survey year.

A. In plots exposed to amb	A. In plots exposed to ambient weather conditions in their first year						
Cover of non-sown species	Cover of non-sown species in the year planted						
Predictor	χ^2	p-value	R ²	Model R ² =0.54			
(Intercept)	36.34	<0.0001					
Year planted	2.44	0.30	0.046				
Seed mix richness	0.51	0.48	0.012				
Echinacea sp. abundance	0.95	0.33	0.028				
P. capillare abundance	15.32	<0.0001***	0.37				
Seed mix * Year planted	1.26	0.53	0.043				
Cover of non-sown species	in the sec	cond year					
Predictor	χ^2	p-value	<i>R</i> ²	Model R ² =0.25			
(Intercept)	72.03	<0.0001					
Year planted	0.14	0.93	0.0080				
Seed mix richness	0.0046	0.95	0.00				
Echinacea sp. abundance	0.30	0.59	0.0060				
P. capillare abundance	2.19	0.14	0.10				
Seed mix * Year planted	4.73	0.094	0.059				
Cover of non-sown species	in the thi	rd year					
Predictor	χ^2	p-value	R ²	Model R ² =0.41			
(Intercept)	150.18	<0.0001					
Year planted	4.02	0.045*	0.23				
Seed mix richness	1.15	0.28	0.023				
Echinacea sp. abundance	0.16	0.69	0.0070				
P. capillare abundance	3.46	0.063	0.26				
Seed mix * Year planted	1.23	0.27	0.022				
Cover of non-sown species	in 2017						
Predictor	χ^2	p-value	<i>R</i> ²	Model R ² =0.29			
(Intercept)	90.81	<0.0001					
Year planted	0.46	0.80	0.020				
Seed mix richness	0.35	0.55	0.0060				
Echinacea sp. abundance	0.028	0.87	0.0010				
P. capillare abundance	0.88	0.35	0.041				
Seed mix * Year planted	4.33	0.11	0.046				

Table 3.5 (cont'd)

	Ū.		1				
Cover of non-sown species in the year planted							
Predictor	χ ²	p-value	<i>R</i> ²	Model R ² =0.39			
(Intercept)	80.45	<0.0001					
Year planted	1.82	0.40	0.034				
Watering treatment	6.35	0.042*	0.086	Tukey post-hoc tests:			
				High-low t=1.63, p=0.24			
				High-mean t=-0.20, p=0.98			
				Low-mean t=-1.83, p=0.17			
Seed mix richness	4.08	0.044*	0.022				
Echinacea sp. abundance	0.012	0.91	0.00				
P. capillare abundance	22.48	<0.0001***	0.21				
Year planted * Watering	5.34	0.25	0.076				
Seed mix * Year planted	1.40	0.50	0.0050				
Seed mix * Watering	2.68	0.26	0.021				
Cover of non-sown species	in the se	cond year					
Predictor	χ^2	p-value	R^2	Model R ² =0.41			
(Intercept)	152.08	<0.0001					
Year planted	12.92	0.0016**	0.063	Tukey post-hoc tests:			
				2014-2015 t=0.029, p=0.96			
				2014-2016 t=-3.97, p=0.0005***			
				2015-2016 t=-5.00, p<0.0001***			
Watering treatment	4.86	0.088	0.058				
Seed mix richness	2.19	0.14	0.013				
Echinacea sp. abundance	0.52	0.47	0.0050				
P. capillare abundance	2.60	0.11	0.029				
Year planted * Watering	4.76	0.31	0.061				
Seed mix * Year planted	6.92	0.031*	0.058				
Seed mix * Watering	8.14	0.017*	0.026				
Cover of sown species in th	ne third ye	ear					
Predictor	χ^2	p-value	<i>R</i> ²	Model R ² =0.30			
(Intercept)	189.85	<0.0001					
Year planted	3.11	0.078	0.058				
Watering treatment	0.74	0.69	0.014				
Seed mix richness	0.14	0.71	0.001				
Echinacea sp. abundance	0.33	0.57	0.005				
P. capillare abundance	1.41	0.24	0.025				
Year planted * Watering	0.89	0.64	0.011				
Seed mix * Year planted	0.029	0.87	0.00				
Seed mix * Watering	3.04	0.22	0.032				

B. In plots receiving watering treatments in their first year

Table 3.5 (cont'd)

Dredictor	v^2	n-value	D ²	Model $P^2 = 0.26$
Fredictor	χ	p-vulue	Λ	Wodel N =0.50
(Intercept)	182.65	<0.0001		
Year planted	13.92	0.00095***	0.073	Tukey post-hoc tests:
				2014-2015 t=2.43, p=0.049*
				2014-2016 t=-2.44, p=0.046*
				2015-2016 t=-4.85, p<0.0001***
Watering treatment	4.03	0.13	0.026	
Seed mix richness	0.26	0.61	0.0020	
Echinacea sp. abundance	0.014	0.90	0.00	
P. capillare abundance	3.36	0.067	0.038	
Year planted * Watering	5.80	0.21	0.039	
Seed mix * Year planted	0.40	0.82	0.0010	
Seed mix * Watering	5.30	0.071	0.035	

Table 3.6. Statistical model results predicting the richness of non-sown species. Linear mixed effect models for ambient first-year plots included a random effect of plot; models for watered first-year plots included random effects of plot and block. *P. capillare* abundance included as a model predictor refers to the abundance of that species in the planting year. *Echinacea sp.* abundance included as a model predictor refers to abundance of that species in the survey year.

A. In plots exposed to ambient weather conditions in their first year						
Richness of non-sown spec	ies in the	year plant	ed			
Predictor	χ^2	p-value	R ²	Model R ² =0.39		
(Intercept)	130.57	< 0.0001				
Year planted	5.19	0.075	0.14			
Seed mix richness	0.16	0.69	0.0050			
Echinacea sp. abundance	0.017	0.90	0.0030			
<i>P. capillare</i> abundance	0.17	0.68	0.010			
Seed mix * Year planted	0.17	0.92	0.0060			
Richness of non-sown spec	ies in the	second ye	ar			
Predictor	χ^2	p-value	R ²	Model R ² =0.067		
(Intercept)	114.28	< 0.0001				
Year planted	0.59	0.75	0.022			
Seed mix richness	0.39	0.53	0.019			
Echinacea sp. abundance	0.0010	0.98	0.00			
<i>P. capillare</i> abundance	0.20	0.65	0.015			
Seed mix * Year planted	0.58	0.75	0.015			
Richness of non-sown spec	ies in the	third year				
Predictor	χ^2	p-value	R ²	Model R ² =0.36		
(Intercept)	151.32	< 0.0001				
Year planted	4.25	0.039*	0.29			
Seed mix richness	0.068	0.79	0.011			
Echinacea sp. abundance	2.52	0.11	0.18			
<i>P. capillare</i> abundance	0.00	0.99	0.037			
Seed mix * Year planted	0.80	0.37	0.062			
Richness of non-sown spec	ies in 201	7				
Predictor	χ^2	p-value	R ²	Model R ² =0.41		
(Intercept)	105.55	<0.0001				
Year planted	2.19	0.34	0.15			
Seed mix richness	0.0001	0.99	0.00			
Echinacea sp. abundance	2.96	0.086	0.16			
P. capillare abundance	1.48	0.22	0.11			
Seed mix * Year planted	0.41	0.82	0.047			

Table 3.6 (cont'd)

	D. III plots receiving water	ing treath			
	Richness of non-sown spec	ies in the	year plant	ed	
	Predictor	χ^2	p-value	R ²	Model R ² =0.19
	(Intercept)	71.00	<0.0001		
	Year planted	0.81	0.67	0.017	
	Watering treatment	2.69	0.26	0.016	
	Seed mix richness	0.99	0.32	0.012	
	Echinacea sp. abundance	0.17	0.68	0.00	
	P. capillare abundance	1.63	0.20	0.022	
	Year planted * Watering	6.55	0.16	0.11	
	Seed mix * Year planted	0.10	0.95	0.001	
	Seed mix * Watering	0.57	0.75	0.007	
Richness of non-sown species in the second year					
	Predictor	χ ²	p-value	R^2	Model R ² =0.19
	(Intercept)	112.49	<0.0001		
	Year planted	1.83	0.40	0.012	
	Watering treatment	0.82	0.66	0.016	
	Seed mix richness	0.16	0.69	0.0020	
	Echinacea sp. abundance	0.0077	0.93	0.0010	
	P. capillare abundance	1.20	0.27	0.018	
	Year planted * Watering	0.78	0.94	0.0060	
	Seed mix * Year planted	0.74	0.69	0.0060	
	Seed mix * Watering	0.43	0.81	0.0060	
	Richness of sown species in	n the third	l year		
	Predictor	χ ²	p-value	<i>R</i> ²	Model R ² =0.19
	(Intercept)	203.84	<0.0001		
	Year planted	2.22	0.14	0.041	
	Watering treatment	1.27	0.53	0.021	
	Seed mix richness	0.77	0.38	0.013	
	Echinacea sp. abundance	0.34	0.56	0.0070	
	P. capillare abundance	0.019	0.89	0.0040	
	Year planted * Watering	0.75	0.69	0.0080	
	Seed mix * Year planted	0.0098	0.92	0.00	
	Seed mix * Watering	0.64	0.73	0.015	
	Richness of sown species in	n 2017			
	Predictor	χ^2	p-value	R^2	Model R ² =0.18
	(Intercept)	143.81	< 0.0001		
	Year planted	0.37	0.83	0.0070	
	Watering treatment	1.92	0.38	0.017	
	Seed mix richness	0.011	0.92	0.00	
	Echinacea sp. abundance	0.18	0.67	0.0030	
	P. capillare abundance	0.23	0.63	0.0020	
	Year planted * Watering	3.70	0.45	0.049	
	Seed mix * Year planted	0.67	0.71	0.0070	
	Seed mix * Watering	0.10	0.95	0.0030	

B. In plots receiving watering treatments in their first year

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LITERATURE CITED

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CHAPTER FOUR

HISTORICAL CONTINGENCY IN ECOLOGICAL RESTORATION: EVIDENCE FROM 83 PRAIRIES

ABSTRACT

Reliable ecological restoration outcomes are of paramount importance to reverse or reduce losses in native biodiversity caused by extensive land use by humans. Yet, restoration outcomes are notoriously variable, reducing public confidence in our ability to restore native biodiversity and its related functions. One commonly assumed source of this variation is weather conditions during the planting year, though empirical evidence for these effects are scarce. Finding evidence for "year effects" in prairie restorations would provide support for historically contingent assembly models, in which early community dynamics impact longer-term community trajectories. It might also suggest ways that subsequent management might mediate these effects and promote higher establishment by native species. Despite experimental evidence for short-term year effects in restoration, their long-term persistence and importance compared to other factors is unclear. The research we report here based on surveys of 83 sites distributed across Illinois, Indiana, and Michigan sheds light on the implications of year effects across a broad geographic gradient. It also allows us to evaluate the persistence of these effects because these restorations had been established for 2-19 years. In 2016, we surveyed plant community composition in the prairies, and considered the interplay between management histories, current community compositions, and the temperature and precipitation in each planting year to ask whether there is a measurable signature of planting-year conditions on present-day plant communities, and what the importance of these effects are compared to other known drivers of restored communities (e.g. seed mix richness, fire frequency). We found that weather conditions in the first growing season explained more variation in the 2016 richness of non-sown species than did site age or fire frequency

across the 83 sites. Sites associated with more precipitation in the planting year had higher richness of non-sown species, community compositions more dissimilar than their seed mixes, and marginally higher non-sown cover. Warmer planting years were associated with increased cover of non-sown species in young sites and decreased cover in older sites. Conversely, prairies planted in cooler years had less non-sown cover in younger sites, and higher non-sown cover in older sites. By using this extensive dataset, we provide evidence that weather conditions during planting years can influence communities that assemble during ecological restoration.

INTRODUCTION

Human impacts on natural ecosystems are a major driver of biodiversity loss worldwide (Foley et al. 2005; Cardinale et al. 2012), and ecological restoration is an important tool for combating this loss (Dobson et al. 1997; Hobbs & Harris 2001; Ruiz-Jaen & Mitchell Aide 2005; Jones et al. 2018). However, outcomes of restoration efforts can vary greatly, with a vast array of possible reasons for this variation including edaphic conditions, invasive species pressure, seed mixes sown, landscape context, land-use history, management decisions, and others (Blumenthal et al. 2003; Averett et al. 2004; Baer et al. 2009; Rowe 2010; Suding 2011; Grman et al. 2015). These drivers represent the suite of deterministic environmental filters that govern community assembly by dictating which species are able to establish and persist at a site given the current conditions (Weiher et al. 2011). However, the establishment history of a community can also affect the outcome of assembly (Fukami 2015). For instance, early arrivers to a community can influence later arrivers through processes such as priority effects (Alford & Wilbur 1985; Fukami et al. 2016; Young et al. 2016) or facilitation (Connell & Slatyer 1977; Grant et al. 2014), leading to disparate communities even when environmental conditions are otherwise the same. In restored systems, the composition of these early arrivers is shaped by the interactions among

restoration methods and site conditions. Much research has assessed the influence of the former, in hopes to quantify best practices for restoration (e.g., Rowe 2010). However, less is known about the effects of different site conditions. In addition, conditions during the planting year, and particularly weather conditions after planting, are likely to have strong effects on restoration outcomes. Though a few token studies and experiments provide evidence that year effects can exist, large-scale assessment across numerous restoration projects is lacking.

These planting year effects (hereafter, year effects) on restored communities make logical sense, but evidence for year effects in the literature is rare, since most restoration projects and ecological studies are not replicated across planting years (Vaughn & Young 2010). In a recent study, we found that different planting years and experimental precipitation regimes significantly altered the seedling emergence patterns of different species, leading to different plant communities in the first growing season of a restored grassland community (Groves & Brudvig 2018). Important work in Kansas and California grasslands has also shown the importance of both planting year (Manning & Baer 2018) and planting year and site conditions (Stuble et al. 2017) on restoration success. This evidence has demonstrated the potential for influence of planting conditions on a community; however, it is unclear how long this influence will last. Evidence that demonstrates year effects over longer time scales is even rarer, with one notable exception finding stark effects: in a grassland restoration experiment in the North American Great Plains, herbicide application on an invasive grass followed by sowing of a native grass was highly successful even a decade later when planted in average or above-average rainfall years, but reverted to dominance by the invasive grass when planted in an exceptionally dry year (Bakker et al. 2003; MacDougall et al. 2008).

Additionally, although these studies support the conclusion that year effects can exist, their relative importance is difficult to study due to the myriad other factors that shape a plant community. Current emphasis on grasslands in the year effect literature likely stems from the accentuated

importance of planting year conditions in highly invaded, highly degraded sites that are restored by intensive vegetation removal efforts followed by sowing seeds of target species, usually within a single season. There is already evidence that restoration outcomes in these systems can be highly influenced by deterministic factors such as soil characteristics, site land use history, management (e.g. prescribed fire frequency), and the richness and density of the seed mix sown (Suding et al. 2005; Piper et al. 2007; Doll et al. 2011; Grman et al. 2013). It therefore remains unknown how important year effects are in context of these other factors known to influence assembly in restored systems. Moreover, there may be an interaction between weather conditions during planting and these other factors; for instance, with site age because of the possibility of decreasing importance of planting year conditions over time, or with soil water holding capacity, because of different effects of rainfall depending on the soil moisture retention at the site.

Finally, it remains unclear exactly what aspects of planting year weather conditions might be most important for subsequent restoration trajectories. Past studies have explored correlations with a limited suite of environmental variables: annual mean temperature, total rainy days (Stuble et al. 2017); June temperature, June-July precipitation (Bakker et al. 2003); and deviations from normal growing season (March-October) precipitation and temperature (MacDougall et al. 2008). Stuble et al. (2017) and MacDougall et al. (2008) notably found no long-term effects of temperature metrics, only precipitation metrics, on plant communities sown in different years. However, the experimental work by Groves & Brudvig (2018) suggested that precipitation, though important, is not the only driver of sown community differences after different planting years. Additional factors are known to be important determinants of seeds breaking dormancy, germinating, and establishing. For instance, warmer temperatures, especially in early mornings or springtime, can advance the phenology of some plant species (Forrest & James 2011), which can favor certain species over others (Wainwright & Cleland 2013). In agronomic systems, temperature-based units such as growing degree days are used to predict
development of plants and other species (Trudgill et al. 2005). Better understanding of which first year weather conditions influence restoration plantings would clarify drivers of variation in restoration outcomes and benefit restoration planning by enabling targeted post-planting restoration actions (i.e., to sites planted in years when such actions would be most beneficial).

The tallgrass prairie is nearly extirpated in North America, with only 0.1% of its original extent remaining (Samson & Knopf 1994). After decades of degradation from intensive agriculture and other human activities, prairie species no longer occur in many landscapes, nor do their seeds persist in the seed bank (Bakker et al. 1996). Therefore, restoration often takes place through seed sowing onto abandoned agricultural lands (Cramer et al. 2008), which could make the establishment of these restored communities particularly susceptible to abiotic and biotic conditions present during their first growing season.

In this study, we surveyed 83 tallgrass prairie restorations to investigate (I) whether planting year conditions related to temperature and precipitation influence the resulting plant community 2-19 years after planting, across a variety of metrics (e.g. species richness and cover of sown and non-sown species), (II) what the relative influence of planting year conditions are compared to other known drivers of variation in restored prairie plant communities (i.e. fire frequency, edaphic conditions, site age, and the richness of the seed mix sown), and (III) whether the influence of planting conditions changes with soil productivity or time since planting. We show that weather conditions have lasting effects on prairie plant communities, particularly through effects on the non-sown species, and that these effects can be of greater magnitude than those of other important drivers of restoration outcomes in this system.

METHODS

Study sites

We surveyed 83 restored prairie sites in Illinois, Indiana, and Michigan July-September 2016 (Figure 4.1). Eighteen of the restored prairie plantings were managed by the McHenry County Conservation District (MCCD) in Illinois (Figure 4.2a). Another 32 sites were managed by The Nature Conservancy's Kankakee Sands Preserve in Indiana (Figure 4.2b). The final 33 sites were scattered across southwest Michigan, installed by the restoration firm Native Connections (Three Rivers, MI) onto properties under various ownership and management (Figure 4.2c). Prairies ranged in size from 0.2-118 hectares and were established with different seeding techniques (broadcast or drill-seeded), and in different planting seasons (dormant or growing season). Sites also differed in previous land use (soy, corn, winter wheat, hay; some converted directly from production, some left fallow), landscape context (forest, agriculture, or other restored prairie sites), soil characteristics (soil water holding capacity ranged from 0.33-0.80, mean 0.50 percent of total soil weight), and planting year (1998-2014). The majority of sites were managed with prescribed fire, with 77% of sites burned within the past 4 years; 20% of sites had not been burned. Seed mixes sown ranged from a richness of 8 to 239 species (mean 57.4 species) and a sowing density of 1.6 to 54.1 kg/ha (mean 9.7 kg/ha).

Field data collection

We visited the 83 restored prairies between 18 July-16 September 2016. In each site, we established a 50 m transect in a random orientation. For Michigan and Illinois sites, transects were centered on the approximate centroid of the site; for Indiana sites, which were much larger, transects were placed inside the boundary of visible edge effects. At 5- or 10- m intervals (for Michigan and Illinois/Indiana sites, respectively), we placed a 1 m x 1 m quadrat frame on the ground and visually

quantified the percent cover of each species present. We surveyed 5 plots per site in Indiana and Illinois, and 10 plots in Michigan (for compatibility with another project outside the scope of this manuscript). In addition, we systematically walked a 20 m x 50 m area centered on the transect and recorded additional species observed. We collected two soil cores at 5 m intervals along each transect using an Oakfield soil probe (20 total per site, 2 cm × 20 cm soil cores). Soil cores were homogenized at each site. We determined soil water holding capacity by saturating field samples and then drying for 72 hours at 105°C and calculating the proportional difference in saturated wet weight and oven-dried weight. Air-dried samples were also analyzed for a variety of soil properties including pH, % organic matter, % clay/silt/sand, and soil nutrients (S, P, Ca, Mg, K, Na, B, Fe, Mn, Cu, Zn, and Al) by the Brookside Laboratories (New Knoxville, OH, USA). To reduce the potential number of predictor variables, we conducted a principal components analysis on the soils data using prcomp in R with each variable scaled due to large variation the concentrations of soil nutrients. For later analyses, we used the first principal component, which accounted for 40.5% of the variation in the soils data and was associated with higher percent organic matter, higher water holding capacity, higher clay content, higher silt content, higher nutrients (except Zn, Fe, and P), and less sand (Table 4.3). Hereafter this first PC axis for soils is referred to as "soil productivity."

Management histories and historical weather data

We worked with the land managers at each site to compile information about the restored prairies, including the date of planting, prescribed fire history, and the relative abundance (by weight) of each species sown in the initial planting. We used 30-arcsec (approximately 800 m) spatially gridded PRISM Climate Data to compile interpolated information on the daily precipitation accumulation and minimum and maximum temperature in the first growing season for each site based on its latitude and longitude (PRISM Climate Group 2018). We used these data to calculate cumulative growing degree days

(base 10°C), cumulative precipitation, and averages related to temperature and precipitation at various stages throughout the growing season.

Statistical analysis

To characterize weather conditions at the time of planting we focused on eleven variables that we hypothesized to influence the germination and establishment of plant communities during the first growing season of prairie restoration: spring temperatures (degree day accumulation March 1 – June 1), spring rainfall (precipitation accumulation March 1 – June 1), summer temperatures (degree day accumulation June 1 – September 1), summer rainfall (precipitation accumulation June 1 – September 1), full growing season temperatures (degree day accumulation March 1 – September 1), full growing season rainfall (precipitation accumulation March 1 – September 1), the hottest month (maximum degree days accumulated in a 30-day period), the longest drought (maximum days without a precipitation event), the driest month (minimum precipitation in a 30-day period, in mm rainfall), average low temperature (March 1 – September 1, °C), and the average monthly rainfall (March 1 – September 1, mm). We focused on this set of variables owing to the reported roles of temperature and precipitation for plant establishment dynamics (e.g., Thompson & Grime 1983; Groves & Brudvig 2018) and for year effects broadly (Bakker et al. 2003; MacDougall et al. 2008; Stuble et al. 2017).

Because many of these variables were correlated (**Figure 4.3**), we conducted a Principal Components Analysis to determine composite metrics with which to test our hypotheses (**Table 4.1**). We focused on the first three axes (out of eleven total) that together accounted for 74.2% of the variation in weather data. The first axis, PC1, accounted for 37.6% of the variation in the weather dataset and positively correlated with all metrics that related to higher temperatures. The second axis, PC2 (22.0% of the variation), was positively correlated with all metrics that related to more rainfall. The third axis, PC3, accounted for 14.7% of the variation in the weather dataset and was negatively associated with summer

precipitation, spring temperatures, and the maximum number of days without a precipitation event, and positively associated with minimum precipitation in a 30-day period and the mean number of rainy days in a 30-day period. We interpret this axis as mild droughts: low overall precipitation that is consistently distributed throughout the growing season, with the worst dry spell relatively wet and short. Plots of the three weather PC axes against the other environmental variables (soils, site age, seed mix richness; also, state) are provided in **Figure 4.7**. The distribution of each variable across sites is provided in **Figure 4.8**.

We used a series of linear models to test for an effect of planting year weather conditions (PC1, PC2, and PC3) on the present-day community. In addition to the three weather PCs, models included the richness of the seed mix, the seeding density (kg/ha), the age of the site in 2016, the frequency of fire (characterized as the years since the last prescribed burn), and soil productivity. None of these variables were colinear, with each correlation coefficient (r) < 0.4 (Mason & Perreault Jr. 1991). Each model also included interactions between PC1, PC2, and PC3 and site age and soil productivity.

Finally, we considered response variables representing typical prairie restoration goals: namely, improving sown species richness and cover and minimizing non-sown species richness and cover. We therefore ran six models, predicting the richness of sown, non-sown, and total species at the site level (20 m x 50 m survey area); the cover of sown and non-sown species at the mean 1 m² plot level; and the Bray-Curtis dissimilarity between the composition of the seed mix sown and the vegetation at the site in 2016 (**Table 4.2**). We compared R² values of predictors in the models to compare their relative influence on planting outcomes.

RESULTS

Total observed species richness in the 83 prairie sites ranged from 23-73 (mean 50); at the plot (1 m²) scale, species richness ranged from 14-48 (mean 28). Sown species richness ranged from 3-35

(mean 18) species at the field scale and from 0-28 (mean 11) at the 1 m² scale. The average percent cover of sown species per plot ranged from 0-106% (mean 51%), while mean non-sown species cover ranged from 2-102% (mean 33%); overlapping individuals allow for sums greater than 100% per plot. The average dissimilarity between the composition of the seed mix and the standing community was 0.69 (range 0.34-1.00); between 0 and 88% of species sown were present at each site.

Effects of planting year on community metrics

We found a significant effect of planting year conditions on plant community metrics (Figure 4.4). The strongest responses were related to the non-sown species: we found that increased precipitation during the first growing season (PC2) was significantly correlated with increased richness of non-sown species (β =2.22, F=7.70, p=0.0072, Figure 4.4A) and marginally correlated with increased cover of non-sown species (β =0.14, F=3.77, p=0.056, Figure 4.4B). Increased planting year precipitation (PC2) was also marginally correlated with decreased richness of sown species (β =-1.30, F=3.40, p=0.070, Figure 4.4C) and was correlated with greater Bray-Curtis dissimilarity between the composition of the seed mix and the 2016 plant community, meaning the communities in prairies planted in wetter years did not resemble their seed mixes as much as prairies planted in drier years (β =0.026, F=6.66, p=0.012, Figure 4.4D).

We also found evidence for a weather by age interaction (**Figure 4.5**), in which warmer planting years (PC1) were associated with higher cover of non-sown species in young sites and less cover in older sites, while prairies planted in cooler years (PC1) had less non-sown cover in younger sites and higher non-sown cover in older sites.

We found no effects of PC3 (mild droughts in planting year) on any 2016 community metrics (**Table 4.4**). We found no significant relationships between weather conditions in the first growing season and sown species cover, sown species richness, or total species richness (**Table 4.4**).

Relative influence of weather compared to known assembly drivers

The variation in non-sown richness that was explained by planting-year precipitation (PC2, $R^2=0.10$, **Figure 4.5**) was greater than the variation explained by fire frequency ($R^2=0.0011$), site age ($R^2=0.00016$), soil productivity ($R^2=0.0016$), seed mix richness ($R^2=0.036$), or seeding density ($R^2=0.052$).

For Bray-Curtis dissimilarity between the seed mix and 2016 community composition, the effect of planting year precipitation (PC2), though significant, was weaker than other predictors. This dissimilarity was better explained by increased seed mix richness (R^2 =0.20, β =0.066, F=16.78, p=0.00012) and older site age (R^2 =0.13, β =0.050, F=10.09, p=0.0023) than increased planting year precipitation (PC2, R^2 =0.092, β =0.026, F=6.66, p=0.012).

Non-sown species cover was best predicted by, listed in decreasing importance: soil productivity (R^2 =0.17, β =0.19, F=13.45, p=0.00049), the interaction between temperature in the first growing season (PC1) and site age (R^2 =0.13, β =0.18, F=9.73, p=0.0027), site age (R^2 =0.084, β =0.27, F=6.02, p=0.017), seed mix richness (R^2 =0.066, β =0.24, F=4.64, p=0.035), and precipitation in the first growing season (PC2, R^2 =0.054, β =0.14, F=3.77, p=0.056).

The cover of sown species was not well predicted by our models (total model R²=0.19), and was best predicted by soil productivity (β =-3.27, F=5.13, p=0.027, R²=0.072). Similarly, sown species richness (total model R²=0.22) was best predicted by the richness of the seed mix (β =3.38, F=8.75, p=0.0043, R²=0.12; total model R²=0.22). We found no significant predictors for overall species richness.

DISCUSSION

Our results show clear evidence for year effects on restored prairie community composition across 83 sites through their effects on the non-sown species. This result is important because the sites surveyed span an extensive gradient of geography (3 states), age (2 to 19 years old), and soil conditions. These year effects were predominantly driven by wetter planting years resulting in higher non-sown species richness and marginally higher non-sown cover. The planting-year effects we detected on nonsown richness were greater than the effects of other known drivers of community establishment in restored prairies (i.e., fire frequency, sown species richness, and soil characteristics).

Sown species richness was marginally decreased following wet planting years (PC2). It is unclear whether this is a result of suppression by the increase in non-sown species that also coincided with wet planting years, or if drier conditions are in fact better for the sown species. We suspect the former, as competition seems a more likely suppressant of sown species establishment than increased water availability. For instance, Groves & Brudvig (2018) found that increased planting-year rainfall increased both sown and non-sown species emergence 3-fold— evidence that sown species do not perform better under drought stress, and that non-sown species increase dramatically under wet conditions.

The second axis of our weather PCA corresponded with increased precipitation accumulation during spring (March 1 – June 1) in addition to increases in the other precipitation-related metrics (**Table 4.1**) A mechanism by which early spring rainfall in particular might increase non-sown while decreasing sown richness is that non-sown species in this system are predominantly exotic and have been demonstrated to exhibit advanced phenology compared with sown native species in this system (Wilsey et al. 2011), and show strong priority effects when competing with native species (Dickson et al. 2012). Further study and direct experimentation will be needed to conclude whether increased precipitation during a prairie's first growing season truly increases weed abundance, and whether the resulting competitive pressures stifle development of the sown community for the long term.

We found that the magnitude of the effect of planting year precipitation on non-sown richness was greater than the effects of known major drivers of community assembly in this system: fire frequency, soil productivity, seed mix richness and density, and site age. Though there was some prior evidence for planting year effects, it was unclear whether these would have minor or major influence on

restoration outcomes. We show that year effects can be large, but are not consistent across all community metrics (e.g. we found no year effects on total species richness or sown species cover).

We predicted that effects of planting year weather conditions might dampen over time as plantings matured and were subjected to ongoing management (i.e. deterministic assembly dependent on environmental filters, Keddy 1992); however, we found no evidence of this, instead finding support for lasting year effects (Vaughn & Young 2010). Additionally, we predicted that effects of planting year conditions, specifically related to precipitation, might be stronger in sites with less productive soils (Heisler-White et al. 2009) because of their decreased ability to maintain water balance during times of water stress; however, we found no evidence for an interaction between year effects and soils, which again emphasizes the importance of planting year conditions across a diversity of site conditions (Stuble et al. 2017).

Because of the increased non-sown and decreased sown richness, wet planting years also correlated with a higher Bray-Curtis dissimilarity between the seed mix composition and the standing vegetation. These results suggest the need for stronger weed control measures following wet planting years and, if possible, support for planting during drier years— a suggestion that previously would have seemed counter-intuitive. Our work contrasts work by Bakker et al. (2003) and MacDougall et al. (2008) which found that a non-sown dominant invader prevailed when restoration occurred in a particularly dry year, which might be a result of climactic differences between our Midwestern sites and the Great Plains, where water may be more limiting, such that drought years more dramatically prevent establishment of sown species.

The impact of planting-year weather patterns on restoration outcomes can also be examined through the lens of future climate projections. In the Midwestern United States, projections are for warmer average temperatures, increased spring rainfall, and decreased summer rainfall (Wuebbles & Hayhoe 2004). A decrease in summer rainfall may not be as much of a burden to newly planted prairie

restorations as an increase in spring rainfall, which in our study was correlated with higher weed pressures that persisted over time, lower richness of sown species, and a vegetation community more dissimilar than the sown seed mix. Our results would therefore suggest an increasing weed burden for prairie restoration practitioners in sites planted under future climate scenarios.

Evidence for lasting planting year effects lends support to historically contingent assembly models (e.g. Fukami 2015), demonstrating that past events can influence the composition of a current community, regardless of deterministic factors like soils or disturbance. Past work has demonstrated the impact of assembly history on experimental communities, including some work in grasslands (e.g., Chase 2003; Martin & Wilsey 2012; Plückers et al. 2013; Helsen et al. 2016; Werner et al. 2016; Young et al. 2016), and a handful of studies have specifically demonstrated year effects in restored grasslands (Bakker & Wilson 2004; MacDougall et al. 2008; Stuble et al. 2017; Groves & Brudvig 2018; Manning & Baer 2018). Our work builds on this body of research by examining the impact of historical contingency across 83 sites that have been restored across time and space, in context of other factors, and in the pragmatic setting of prairies restored by practitioners.

Our work also contributes important understanding to the question of why restoration outcomes vary, showing that both stochastic (weather) and deterministic factors (mix richness, soil productivity) factors have roles to play. The marrying of these two principles has been important to community ecology over the past decade (Adler et al. 2007; Chase 2007; Chase & Myers 2011; Myers & Harms 2011); we show how they apply to restoration with important implications for interpreting restoration outcomes.

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APPENDIX

Figures



Figure 4.1 Map of study sites.

(A)







(C)



Figure 4.2. Photos of restored prairies. (A) Marengo Ridge (planted 2009), McHenry County, Illinois on September 13, 2016. (B) Kankakee Sands Preserve unit J (planted 2009), Newton County, Indiana on September 8, 2016, and (C) Ed Lowe Foundation (planted 2011), Cass County, Michigan on July 27, 2016.



Figure 4.3. Scatter plots and pairwise correlations (r) between weather variables.



Figure 4.4. Significant effects of planting year weather on restoration outcomes. We found an effect of planting year weather (PC2: rainfall) on (A) the richness of non-sown species (1000 m² site), (B) the cover of non-sown species (mean 1 m² plot), (C) the richness of sown species (1000 m² site), and (D) on the Bray-Curtis dissimilarity between the seed mix and the 2016 vegetation composition.



Figure 4.5. The effect of planting year temperature (weather PC1) on 2016 non-sown species cover (mean 1 m² plot) varied depending on site age. For plotting, sites within one standard deviation from the average PC1 value were assigned the "average" category (58 sites). Sites more than one standard deviation above average were assigned "warmest: (11 sites); sites more than one standard deviation below average were assigned "coolest" (14 sites).



Figure 4.6. The relative importance of weather conditions and other factors on different measures of **restoration outcomes across 83 restored prairies in the Midwestern USA.** Each panel shows the standardized regression coefficients with 95% confidence intervals for each continuous predictor. Models included interactions between weather PC1, PC2, PC3 and both site age and soil productivity. Interaction effects and the rest of the full statistical results are reported in **Table 4.4**.



Figure 4.7. Scatter plots of the three PC axis rotations of weather variables against each prairie assembly predictor. PC axis 1 (temperature) is plotted against (A) site age, (B) seed mix richness, (C) state, (D), soil productivity, (E) seeding rate, and (F) years since last prescribed fire; PC axis 2 (rainfall) is likewise plotted against (G) site age, (H) seed mix richness, (I) state, (J), soil productivity, (K) seeding rate, and (L) years since last prescribed fire; and PC axis 3 (mild droughts) is plotted against (M) site age, (N) seed mix richness, (O) state, (P), soil productivity, (Q) seeding rate, and (R) years since last prescribed fire.

Figure 4.7 (cont'd)









Figure 4.8. Distributions of weather and site condition variables across sites.

Figure 4.8 (cont'd)







Figure 4.8 (cont'd)





Table 4.1. Weather variable rotations for PC axes 1, 2, and 3. Values > |0.3| are denoted in bold for

emphasis.

	PC1 (temperature)	PC2 (rainfall)	PC3 (mild droughts)
Spring weather (March 1 – June 1)			
Degree day accumulation	0.28	0.28	-0.37
Precipitation accumulation	-0.20	0.37	-0.056
Summer weather (June 1 - September 1)			
Degree day accumulation	0.44	0.058	0.17
Precipitation accumulation	-0.19	0.35	-0.33
Total growing season weather (March 1 – September 1)			
Degree day accumulation	0.47	0.17	-0.054
Precipitation accumulation	-0.25	0.49	-0.24
Mean low temp	0.39	0.33	-0.15
Growing season extremes			
Maximum degree days in a 30-day period	0.45	0.022	0.13
Minimum precipitation in a 30-day period	-0.10	0.32	0.52
Maximum number of days without a precipitation event	-0.036	-0.26	-0.48
Mean number of rainy days per 30-day period	-0.12	0.34	0.35

Tables

 Table 4.2. Six variables used as response metrics to evaluate effects of planting year weather

conditions and other assembly drivers on prairie restoration outcomes.

Restored prairie response variables
Site level (1000 m ² survey area)
Richness of sown species
Richness of non-sown species
Total species richness
Plot level (mean 1 m ²)
Cover of sown species
Cover of non-sown species
Bray-Curtis dissimilarity between the composition of
the seed mix sown and the vegetation at the site

Table 4.3. Soil variable rotations for PC axis 1. PC axis 1 accounted for 40.5% of the variation in the soils

data. PC axis 2 accounted for 15.4%, PC axis 3 accounted for 12.0%.

	PC1
рН	0.15
Soil organic matter	0.28
S (ppm)	0.081
P (mg/kg)	-0.14
Ca (mg/kg)	0.31
Mg (mg/kg)	0.33
K (mg/kg)	0.23
Na (mg/kg)	0.17
B (mg/kg half detection)	0.28
Fe (mg/kg)	-0.13
Mn (mg/kg)	0.22
Cu (mg/kg half detection)	0.29
Zn (mg/kg)	-0.027
Al (mg/kg)	0.045
Water holding capacity	0.29
% Clay	0.31
% Silt	0.28
% Sand	-0.31

Table 4.4. Complete statistical results for models analyzing the relative importance of weather

conditions and other factors on prairie restoration outcomes. Asterisks denote statistical significance at

p<0.05.

A. Species richness (1000 m ² site)			٨	<i>Model R</i> ² =0.24
Predictor	в	F	p-value	<i>R</i> ²
Weather PC1 (temperature)	-0.11	0.019	0.89	0.0075
Weather PC2 (precipitation)	0.92	0.86	0.36	0.0020
Weather PC3	0.056	0.0020	0.96	0.048
Seed mix richness	1.36	0.72	0.40	0.00070
Seeding density	3.40	2.65	0.11	0.032
Years since last fire	-1.23	0.71	0.40	0.017
Soil productivity	-0.035	0.0022	0.96	0.00030
Site age	0.16	0.011	0.92	0.0022
Weather PC1 (temperature) X Site Age	0.42	0.27	0.61	0.0010
Weather PC2 (precipitation) X Site Age	-1.36	1.18	0.28	0.025
Weather PC3 X Site Age	0.016	0.0001	0.99	0.029
Weather PC1 (temperature) X Soils	0.39	2.71	0.10	0.097
Weather PC2 (precipitation) X Soils	0.33	0.82	0.37	0.011
Weather PC3 X Soils	0.0071	0.0001	0.99	0.023
B. Sown species richness (1000 m ² site)			/	Model R ² =0.22
Predictor	в	F	p-value	R^2
Weather PC1 (temperature)	-0.23	0.17	0.68	0.0026
Weather PC2 (precipitation)	-1.30	3.40	0.070	0.049
Weather PC3	1.04	1.35	0.25	0.020
Seed mix richness	3.38	8.75	0.0043**	0.12
Seeding density	0.20	0.018	0.89	0.00028
Years since last fire	-0.91	0.76	0.39	0.011
Soil productivity	-0.23	0.19	0.66	0.0029
Site age	0.29	0.067	0.80	0.0010
Weather PC1 (temperature) X Site Age	-0.28	0.22	0.64	0.0034
Weather PC2 (precipitation) X Site Age	0.38	0.18	0.67	0.0028
Weather PC3 X Site Age	-0.53	0.30	0.59	0.0045
Weather PC1 (temperature) X Soils	0.090	0.28	0.60	0.0042
Weather PC2 (precipitation) X Soils	0.24	0.88	0.35	0.013
Weather PC3 X Soils	0.057	0.018	0.89	0.00028
<i>C.</i> Non-sown species richness (1000 m ² site)			٨	Aodel R ² =0.24
Predictor	в	F	p-value	R^2
Weather PC1 (temperature)	0.12	0.038	0.85	0.00058
Weather PC2 (precipitation)	2.22	7.70	0.0072**	0.10
Weather PC3	-0.98	0.94	0.34	0.014
Seed mix richness	-2.02	2.44	0.12	0.036
Seeding density	3.20	3.59	0.062	0.052
Years since last fire	-0.32	0.073	0.79	0.0011
Soil productivity	0.20	0.11	0.74	0.0016

Table 4.4 (cont'd)

Site age	-0.13	0.011	0.92	0.00016
Weather PC1 (temperature) X Site Age	0.70	1.12	0.29	0.017
Weather PC2 (precipitation) X Site Age	-1.74	2.98	0.089	0.043
Weather PC3 X Site Age	0.54	0.25	0.62	0.0037
Weather PC1 (temperature) X Soils	0.30	2.48	0.12	0.036
Weather PC2 (precipitation) X Soils	0.085	0.083	0.77	0.0013
Weather PC3 X Soils	-0.050	0.011	0.92	0.00017
D. Cover of sown species (1 m^2 plots)			Мос	lel R ² =0.19
Predictor	в	F	p-value	R ²
Weather PC1 (temperature)	-2.11	1.99	0.16	0.029
Weather PC2 (precipitation)	-2.16	1.23	0.27	0.018
Weather PC3	2.13	0.75	0.39	0.011
Seed mix richness	-1.62	0.27	0.61	0.0040
Seeding density	0.065	0.0003	0.99	<0.0001
Years since last fire	-2.77	0.94	0.34	0.014
Soil productivity	-3.27	5.13	0.027*	0.072
Site age	-2.10	0.46	0.50	0.0069
Weather PC1 (temperature) X Site Age	-2.56	2.57	0.11	0.037
Weather PC2 (precipitation) X Site Age	1.54	0.40	0.53	0.0060
Weather PC3 X Site Age	1.29	0.23	0.63	0.0035
Weather PC1 (temperature) X Soils	-0.15	0.097	0.76	0.0015
Weather PC2 (precipitation) X Soils	0.55	0.60	0.44	0.0090
Weather PC3 X Soils	-0.28	0.058	0.81	0.00087
E. Cover of non-sown species (1 m^2 plots) (log transformed) Model R^2 =0.40				del R ² =0.40
Predictor	в	F	p-value	<i>R</i> ²
Weather PC1 (temperature)	0.085	2.50	0.12	0.037
Weather PC2 (precipitation)	0.14	3.77	0.056	0.054
Weather PC3	0.032	0.13	0.72	0.0020
Seed mix richness	0.24	4.64	0.035*	0.066
Seeding density	-0.062	0.18	0.67	0.0027
Years since last fire	0.077	0.56	0.46	0.0084
Soil productivity	0.19	13.45	0.00049***	0.17
Site age	0.27	6.02	0.017*	0.084
Weather PC1 (temperature) X Site Age	0.18	9.73	0.0027**	0.13
Weather PC2 (precipitation) X Site Age	-0.044	0.24	0.62	0.0037
Weather PC3 X Site Age	-0.026	0.072	0.79	0.0011
Weather PC1 (temperature) X Soils	0.012	0.53	0.47	0.0080
Weather PC2 (precipitation) X Soils	-0.020	0.60	0.44	0.0090
Weather PC3 X Soils	0.0012	0.0008	0.98	<0.0001
	F. Bray-Curtis dissimilarity between seed mix and 2016 vegetation		Model R ² =0.54	
F. Bray-Curtis dissimilarity between seed mix	and 2016 v	egetation	IVIOC	IEI K -0.54
F. Bray-Curtis dissimilarity between seed mix Predictor	and 2016 v в	egetation F	p-value	R^2
<i>F. Bray-Curtis dissimilarity between seed mix</i> <i>Predictor</i> Weather PC1 (temperature)	and 2016 v 6 0.012	egetation F 2.40	<i>p-value</i> 0.13	$\frac{R^2}{0.035}$
<i>F. Bray-Curtis dissimilarity between seed mix</i> <i>Predictor</i> Weather PC1 (temperature) Weather PC2 (precipitation)	and 2016 v 6 0.012 0.026	egetation F 2.40 6.66	<i>p-value</i> 0.13 0.012*	<i>R</i> ² 0.035 0.092
<i>F. Bray-Curtis dissimilarity between seed mix</i> <i>Predictor</i> Weather PC1 (temperature) Weather PC2 (precipitation) Weather PC3	and 2016 v <u>6</u> 0.012 0.026 -0.0075	2.40 6.66 0.36	<i>p-value</i> 0.13 0.012* 0.55	<i>R</i> ² 0.035 0.092 0.0055

Table 4.4 (cont'd)

Seeding density	-0.012	0.35	0.55	0.0053
Years since last fire	0.0082	0.31	0.58	0.0048
Soil productivity	0.011	0.024	0.88	0.0036
Site age	0.050	10.09	0.0023**	0.13
Weather PC1 (temperature) X Site Age	0.0068	0.70	0.41	0.022
Weather PC2 (precipitation) X Site Age	-0.0054	0.19	0.67	0.025
Weather PC3 X Site Age	0.00041	0.0009	0.98	0.00090
Weather PC1 (temperature) X Soils	0.0029	1.47	0.23	0.022
Weather PC2 (precipitation) X Soils	-0.0048	1.69	0.20	0.025
Weather PC3 X Soils	-0.0014	0.060	0.81	0.00090

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CHAPTER FIVE

CONCLUDING REMARKS

This dissertation has sought to strike a balance between research that could inform restoration and research that could inform ecological theory. The study of planting year effects on community assembly provides a framework upon which tests of historically contingent assembly can be merged with practical, mechanistic questions that could be of more immediate interest to restoration practitioners.

Through a four-year field experiment at the Kellogg Biological Station's Lux Arbor Reserve, we were able to find evidence to support the year effect concept. We were also able to disentangle the mechanistic considerations of the influence of precipitation versus other weather conditions, and the impacts of weather on the germination of seeds versus the survival of seedlings. We learned, by directly watering experimental plots, that increased rainfall increased the number of seeds that emerged from both the sown seed mix and the weed seed bank, and that this increase was particularly dramatic for weed species. Watering did not, however, affect the identities of the species that emerged. Instead, different communities arose in three different planting years that had different weather conditions— even when comparing among plots that received the same watering treatment in each planting year. This suggests that conditions besides rainfall, such as temperature, dictate which sown and non-sown species will establish in the first year of a prairie restoration. Understanding these planting-year differences were an important first step toward understanding how year effects operate in this system. Without this evidence for community differences in the first growing season, there would be no basis from which different community assembly trajectories could be catalyzed by planting year conditions, and no biological mechanism by which year effects could occur.

Differences among prairies in their first growing season did not alone constitute a year effect, however, which is why we followed these prairies into their second, third, or fourth growing seasons. We saw the cover and richness of sown species fluctuate each year, seemingly responding to current conditions regardless of the prairie's age or original planting conditions. But the cover of non-sown species remained significantly different across the prairies planted in different years, as did the overall community composition, despite the prairies being initially planted using the same mix and the same methods at the same site. This provides evidence that differences in first-year emergence patterns can indeed lead to continuing year effects.

Throughout this experiment, we found no evidence that increased seed mix richness mitigated any adverse impacts of weather conditions. We predicted that sowing a greater number of species, much like diversifying a portfolio, would increase the total number of species that would be successful under any given conditions, and therefore increase the overall success of a planting (i.e. increasing species richness and cover). Although we found increases in the number of sown species with increased mix richness, a higher richness mix did not lead to an increased quantity of sown species under any planting conditions. In addition, it seems that if species in a high richness mix are not chosen carefully, an increase in richness (if seeding density is held constant) could possibly take away individuals from species that are more consistent in their emergence across a variety of weather conditions. Practitioners likely already deal with this tradeoff between rarity and likelihood of establishing when considering species for inclusion in a high diversity mix.

Our final endeavor was to learn whether the results from this relatively small scale, highly controlled field experiment would be relevant to restored prairies of different ages, larger sizes, different geographic locations, and diverse prairie management strategies. We surveyed 83 restored prairies that ranged from 2-19 years old in Illinois (McHenry County Conservation District), Indiana (Nature Conservancy's Kankakee Sands Reserve), and Michigan (private plantings restored by Native
Connections) to look for signatures of planting year conditions on the present-day plant communities. Despite the variation in landscapes, soils, seed mixes, ages, and management decisions across the prairies, we found that the best predictor of the richness of non-sown species was precipitation in the planting year— even when compared to predictors like prescribed fire frequency, soil productivity, or site age. Increased planting year rainfall was also marginally correlated with decreased sown species richness and increased non-sown species cover. Prairies planted in rainier years were also found to be less similar in composition to their seed mixes than those planted in drier years. In general, wet planting years led to worse prairie restoration outcomes.

There are at least two ways to synthesize these results. In the first scenario, increased planting year precipitation acts through increases in the abundance of weeds during the first growing season. The dominant weeds in a young prairie are typically ruderal species that drop out in future years, so their identities in this scenario (which vary with non-precipitation metrics such as temperature) are irrelevant. The increased density of a flush of ruderal weeds, despite its transience, suppresses the establishment of target species in a way that leaves the prairie vulnerable to a future of continually elevated non-sown species pressures. In some cases, aggressive perennials are also present in a young prairie, and increasing their numbers increases their ability to exert priority and maintain their foothold into the future, directly adding to the future non-sown community.

An alternate scenario is that different first-year community compositions are indeed the catalyst for lasting year effects, but that the quantity of water hitting the ground does not capture the influence of a rainy season on the identities of emerging plants. Increased precipitation across a growing season could be associated with any number of other weather conditions or biotic influences besides rainfall per se: greater cloud cover, increased humidity, increased fungal pathogen loads, different behavioral patterns of granivores or herbivores, and much more. Therefore, it is possible that the year effects we demonstrated in our field experiment (i.e., different community compositions across three planting

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years when watering treatment was held constant) were still caused by something linked to the raininess of that season, despite maintaining a constant amount of watering in each year. In this scenario, a more traditional historically contingent assembly model can be invoked, in which the different species identities early in community assembly dictate which species are able to establish and persist over time. In this case, the species that establish in a rainy planting year are more conducive to the long-term establishment of non-sown species than are the species that establish in a drier year.

Although the first scenario is mechanistically more appealing, evidence from our experiment suggests the second scenario is more likely. This is because we did not find any impacts of first year watering treatment on the communities that we followed over time, which we would have expected if the increase in first year weed abundance was the catalyst for different community assembly trajectories.

Regardless of the mechanistic explanation for how year effects occur, finding a correlation between any planting year weather condition and the present-day community (up to 19 years later) across such a diverse spectrum of sites is noteworthy, and gives concrete support for historically contingent models of community assembly. Under these models, the outcome of community assembly is altered depending on what happened earlier in assembly—like the establishment of different species, or a flush of weeds at the outset of a restoration project. Although it increasingly seems that any ecological conclusion other than "it depends" is rather suspect, our results do provide strong evidence that historically contingent processes can exert a real force on community assembly in this system.

For restoration practitioners, we may not have unlocked any great secrets of restoration. I would surmise that most Midwestern prairie restoration managers are already operating at full weed suppression capacity, and learning that a wet planting year makes weedier prairies will not be terribly helpful until we can predict annual weather patterns. Even then, only the most fortunate practitioners will likely have the resources and time necessary to stall restoration activities for an entire year or more

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until conditions improve. That said, understanding that non-sown species pressures could be particularly and continuously high in prairies restored under wetter conditions could prepare practitioners to allocate more resources toward aggressive weed control measures for those sites, such as mowing or herbicide application.

In the end, it is this author's hope that these six years of graduate study have contributed some incremental step forward in understanding historically contingent assembly models as well as variation in tallgrass prairie restoration outcomes. Future research should continue to explore the mechanisms by which year effects occur. Specifically, a direct test of the effects of different temperatures on first year community establishment, plus a direct test of the effects of increased weed abundance (compared to different weed identities) on sown species and general community establishment over time would add clarity to the ideas presented here.

Thanks for reading.