




Species diversity and dispersal traits alter biodiversity spillover in reconstructed grasslands

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Abstract

1. Grasslands are among the planet's most imperilled ecosystems, largely because habitat conversion has caused extreme biodiversity loss. In response, managers and scientists aim to recreate grassland habitat, yet these reconstructed grasslands are often species-poor and lose diversity through time. One potential mechanism to promote biodiversity in grasslands is spillover, or the targeted dispersal of species across habitat boundaries from areas of high to low biodiversity. There is potential for native species to disperse via spillover from high-quality remnant habitat and establish in reconstructions, thus increasing biodiversity. However, plant dispersal and establishment are often context dependent, and the conditions that promote spillover in grasslands are largely unknown.
2. Here we examine the contexts under which spillover can enhance biodiversity in grasslands. Specifically, we investigate whether the species richness of reconstructions and individual plant dispersal traits alter spillover. To do so, we surveyed plant species richness at reconstructed grasslands of varying diversity adjacent to remnant grasslands.
3. We found that spillover from remnants supplies reconstructions with rare species that would otherwise not be present, but only in reconstructions with lower overall richness. Furthermore, spillover was more likely to occur for species with wind dispersed seeds than species with unassisted seed dispersal.
4. *Synthesis and applications.* Our results show that the context dependency of both dispersal and establishment processes are critical to understanding when and where spillover can promote biodiversity in reconstructed systems. Understanding these contexts will help land managers leverage natural dispersal to mitigate biodiversity loss by anticipating which species are likely to arrive in reconstructions without assistance and when they are likely to establish.

KEYWORDS

biodiversity, dispersal, establishment, grasslands, habitat reconstruction, land management, life-history traits, spillover

1 | INTRODUCTION

Biodiversity loss due to fragmentation and land use alteration is of increasing global concern (Barnosky et al., 2011; Fahrig, 2003), with grassland systems being among the most impacted (Newbold et al., 2016). To mitigate the negative effects of this loss, restoration projects turn converted lands back into grassland habitat in an effort to recreate the high diversity and functionality of remnant, or unconverted, systems (Hallett et al., 2013). However, reconstructed grasslands, or those that were restored directly from agricultural fields (Kurtz, 2013), are commonly species-poor in comparison to their remnant counterparts (e.g. Barak et al., 2017; Martin, Moloney, & Wilsey, 2005), and tend to lose diversity through time (Baer, Blair, & Collins, 2016; Sluis, 2002). Understanding mechanisms that maintain high biodiversity, specifically dispersal and establishment (Sullivan, Clark, Tilman, & Shaw, 2018), could promote higher diversity in these chronically degraded systems (Newbold et al., 2016; Wright & Wimberly, 2013).

One potential way to increase grassland biodiversity is through "spillover", or the natural dispersal of species across habitat boundaries (McClanahan & Mangi, 2000; Roberts, Bohnsack, Gell, Hawkins, & Goodridge, 2001; Rowley, 1994). Spillover can provision ecosystem services like biodiversity, especially when organisms move from higher quality habitat where population sizes tend to be larger and more diverse. In marine habitats, fish spillover from protected areas can improve catch rates in adjacent fisheries (e.g. McClanahan & Mangi, 2000; Roberts et al., 2001), whereas in croplands, beneficial insect spillover from forests can increase pollination and pest consumption by natural enemies (Rand, Tylianakis, & Tscharnke, 2006; Ricketts, 2004). Spillover can also increase native biodiversity in terrestrial systems when propagules are exchanged, through dispersal and establishment, between adjacent high- and low-quality areas. For example spillover can occur from remnant forests to adjacent plantation (e.g. Matlack, 1994; Vespa, Zurita, Gatti, & Bellocq, 2018; Wunderle, 1997), recently reforested habitat (Brunet & Von Oheimb, 1998), or from restored to degraded savannas (Brudvig, Damschen, Tewksbury, Haddad, & Levey, 2009; Turley, Orrock, Ledvina, & Brudvig, 2017). The potential exists for spillover to similarly increase biodiversity in the degraded grasslands of the American Midwest, where spillover studies are rare (but see Kindscher and Tieszen (1998)).

Spillover is likely to increase biodiversity in reconstructed grasslands because reconstructions are often dispersal limited. When highly diverse seed mixes are seeded into established reconstructions, the species richness of the reconstructions tend to increase as a result (e.g. Foster, 2001; Foster & Tilman, 2003). This suggests that reconstructed grasslands have the capacity for greater biodiversity but lack a sufficient source of diverse propagules. Moreover, work on European grasslands has shown reconstructions to be dispersal limited, and that close proximity to source populations of native plant species increases reconstruction diversity (Bischoff, Warthemann, & Klotz, 2009; Cousins & Lindborg, 2008; Öster, Ask, Cousins, & Eriksson, 2009; Winsa, Bommarco, Lindborg, Marini, & Öckinger, 2015). Despite its applicability, the framework of spillover

has yet to be explicitly applied to the reconstructed grasslands of the American Midwest, where we expect a similar pattern. Here, proximity to remnants could help ameliorate dispersal limitation in reconstructions via spillover. Understanding spillover in reconstructed grasslands would provide a greater understanding of how natural dispersal promotes biodiversity in these systems, which could in turn readily influence management decisions.

However, predictions of the overall effectiveness of spillover for promoting grassland biodiversity are complicated by the fact that grassland plant species tend to exhibit context dependency in both dispersal and establishment processes. The local environment (Marchetto, Jongejans, Shea, & Isard, 2010; Teller, Campbell, & Shea, 2014), as well as individual plant traits (Moles & Westoby, 2004; Thomson, Moles, Auld, & Kingsford, 2011) can alter a species' dispersal ability. Indeed, dispersal traits are known to be important to spillover. For example plant biodiversity spillover into longleaf pine savanna is most common for species with animal dispersed seeds (Brudvig et al., 2009), and fish spillover from marine protected areas is greatest for species with moderate dispersal (McClanahan & Mangi, 2000). In open grassland systems where wind dispersal dominates (Collins & Uno, 1985) we might expect the effects of spillover to be stronger for species with wind or unassisted dispersal as opposed to those with animal dispersal (Damschen et al., 2008). Additionally, context dependency can also influence establishment, as increased species richness in grasslands tends to decrease establishment ability of novel species (e.g. Fargione & Tilman, 2005; Kennedy et al., 2002) through alterations to assembly history (Martin & Wilsey, 2012) or decreased niche space (J. Fargione, Brown, & Tilman, 2003). Successful spillover requires the establishment of native plants into reconstructed grasslands where they have been locally extirpated, thus the diversity of the reconstructed grasslands accepting propagules might also alter the effects of spillover. Despite this, comparable "spillover" studies tend to investigate receiving habitats with relatively low diversity (Bischoff et al., 2009; Cousins & Lindborg, 2008; Helsen, Hermy, & Honnay, 2013; Öster et al., 2009; Winsa et al., 2015). These studies looked at the establishment of novel species into habitats with richness ranging from four (Cousins & Lindborg, 2008) to 15 species (Winsa et al., 2015). However, increased seeded diversity in grassland reconstructions has become a much more common practice; in the American Midwest current seed mixes for grassland reconstructions are on the order of roughly 30 species (John Voz, pers. comm.) To better understand how spillover can increase diversity in reconstructed grasslands it is therefore necessary to examine a wider range of seeded species richness. Put together, the context dependency of both dispersal and establishment are critical to understanding when and where spillover can promote biodiversity in grassland systems.

Here we investigate the contexts under which spillover can enhance biodiversity in reconstructed grasslands. Specifically, we ask (a) does spillover occur from remnant to reconstructed grasslands? (b) Does the diversity of reconstructed grasslands alter the effects of spillover? And (c) does the likelihood that any given species will spill over depend on its dispersal traits? Here, we address a gap in

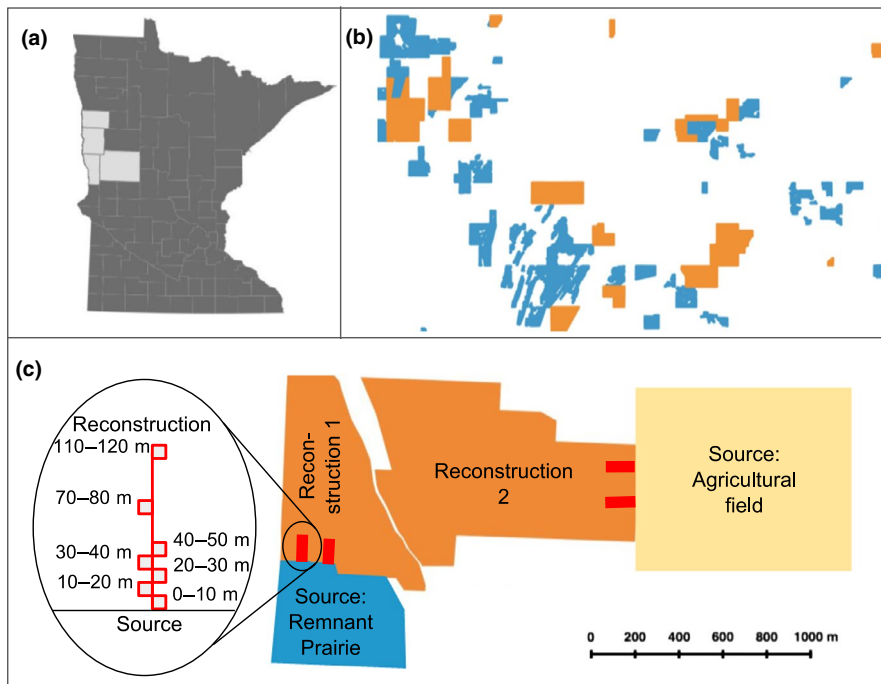


FIGURE 1 Study area and sampling design. (a) Minnesota counties where we conducted surveys are highlighted in light grey: Norman, Clay, Wilkin and Otter Tail. (b) A representational view of the mosaic of remnant (blue) and reconstructed (orange) grasslands. This view is of south-eastern Norman County. (c) Our sampling design. Two transects, in red, start at the boundary of each source and extend 120 m into the reconstructions. On the left, an enlarged transect demonstrates our sampling plots where we conducted our vegetation surveys. We surveyed 15 sites; eight remnant-adjacent reconstructions and seven agriculture-adjacent reconstructions

our understanding of how plant traits and reconstructed community richness affect spillover in grassland systems, allowing for better estimates of when and where we can expect spillover to increase biodiversity in degraded grasslands. To answer these questions, we study spillover of native species between adjacent remnant and reconstructed grasslands in northwest Minnesota. We find that both reconstruction diversity and dispersal mode affect spillover, with spillover only occurring in reconstructions of low species richness and occurring more frequently for wind dispersed species, with a trend towards increased spillover with animal dispersed species. Our results are likely to scale to the greater American Midwest where the mosaic of remnant and reconstructed grasslands provides an ideal system for natural increases in native biodiversity due to spillover.

2 | MATERIALS AND METHODS

2.1 | Site selection

We conducted our research in the Red River Valley of northwest Minnesota (Figure 1a) from July 26th to September 8th, 2017. Selected sites were directly adjacent remnant and reconstructed grasslands (Figure 1b), where the remnant could serve as the source habitat for the spillover of diverse propagules into the reconstructed grassland. After establishment, none of the reconstructions included in our study are regularly grazed or mowed, as is typical of grasslands in the American Midwest since the loss of bison from this ecosystem (Knapp et al., 1999). All reconstructions were directly converted from agricultural fields to ensure the seed bank was eliminated prior to the reconstruction planting. For all reconstructions included in our study, seed lists for the species sown during reconstruction were obtained from the Minnesota Board of Soil and Water Resources.

We chose sites where the seeded species richness of reconstructions was both high (14–37 species, created from 2007 and 2012) and low (1–6 species, created from 1987 and 1999) to determine how the diversity of reconstructions altered spillover. Seeded species richness directly correlated with the established species richness in our 2017 surveys ($p < .001$, $r^2 = .574$), where the mean number of established species in low and high diversity reconstructions were 17.3 ± 6.1 and 32.8 ± 6.9 species respectively. Thus, hereafter we refer to sites as differing by species richness. We also selected sites where reconstructions were adjacent to agricultural fields to control for edge effects and background levels of stochastic dispersal and establishment. Here, the agricultural source habitat could not provide diverse, native propagules to move into the reconstructions. In total, we had 15 sites – eight remnant-adjacent reconstructions with high ($n = 4$) and low ($n = 4$) species richness, and seven agriculture-adjacent reconstructions with high ($n = 4$) and low ($n = 3$) species richness. To confirm this design, an additive ANOVA demonstrated that there was no difference in the established species richness of reconstructions adjacent to remnants versus agricultural fields ($df = 1$, residual $df = 12$, $F = 2.45$, $p = .144$), but diversity treatments were significant different from each other ($df = 1$, residual $df = 12$, $F = 18.74$, $p = .001$).

2.2 | Data collection

To determine the pool of species that could exhibit spillover into the reconstructed grasslands we surveyed species in the remnant and agricultural source habitats. We surveyed the areas of remnant grasslands adjacent to the reconstructions with an adapted random walk method (Rew, Maxwell, Dougher, & Aspinall, 2006). We walked into and throughout the remnant, listing every plant species found

until no new species had been identified for ten minutes. We surveyed source agricultural habitats by identifying the plant species inhabiting the field (crop type) and the field border. We surveyed the plant composition of reconstructions using two 120 m transects starting at haphazardly selected locations and extending perpendicular to the reconstruction-source habitat boundary (Figure 1c). Along each transect we surveyed plant species richness within seven 10×10 m (100 m^2) plots, placed at 0, 10, 20, 30, 40, 70 and 110 m (Figure 1c). Within each plot we walked throughout and identified all vascular plants to species, making sure to survey close to the ground to identify smaller plants and seedlings. For unidentifiable plants, samples were taken and their presence recorded. We then identified samples of unknown species in the laboratory using keys. All samples were keyed to species, except for the genus *Juncus*, which we identified at the genus level. The length of our transects ensured we surveyed appropriate distances to capture spillover events (Brudvig et al., 2009; Kindscher & Tieszen, 1998).

2.3 | Statistical analysis

We were specifically concerned with the need for increasing native diversity in reconstructed grasslands through spillover. Therefore, we defined spillover as the dispersal and establishment of desirable native species into reconstructed grasslands from a source habitat. To show evidence of spillover we required that (a) individual species must have arrived from outside sources, (b) species are native and found in high-quality grassland habitats (based on those in Packard and Mutel (1997)) and (c) overall, there is a negative relationship between the richness of these incoming desirable species and distance from the source habitat (e.g. Brudvig et al., 2009). Prior to analysing the reconstructed grassland data, we removed all species that were included in the original seed mix at the site level, as it would be impossible to tell if these species moved into the reconstruction via spillover or simply arose from the seed bank. Then, we pared down the remaining species to those found in grassland habitats (Packard & Mutel, 1997). From this list, we also removed four species (*Solidago canadensis*, *Solidago gigantea*, *Symphyotrichum ericoides* and *Symphyotrichum lanceolatum*) that were nearly ubiquitous across all sites and distances yet were never included in a seed mix, leading us to believe they already had strong colonization ability. We termed this pared list as “desirable species” (Table S1).

To determine (a) if spillover occurred, and if so (b) how the diversity of reconstructed grasslands altered spillover, we consider how the number of desirable species changes with distance from the source border. Initially we used a linear model across all distances, but evaluation of residuals suggested a lack of fit. Therefore, we used a “broken-stick” model with a negative linear fit for average desirable species richness through c. 50 m from the source border, beyond which the average is approximately constant. To describe spillover for each combination of reconstruction diversity and adjacent source habitat type, we fit a random coefficient regression model to the data up to 50 m from the source border. This is a linear mixed effect model with a linear

effect of distance and a different mean intercept and mean slope for each combination of reconstruction diversity and source type. Site-specific variability in the intercept and slope was accounted for by potentially correlated random effects for the site-specific intercepts and slopes (Harrison et al., 2018). We accounted for multiple transects within fields by averaging. That is we considered transects as subsamples within each primary sampling unit and averaged number of desirable species at the same distances within each site. This approach considerably simplifies the random effects model and focuses attention on the variation between the primary sampling units (Murtaugh, 2007). The effect of primary interest is the three-way interaction between the fixed effects of source type (remnant vs. agriculture), reconstruction species richness (high vs. low) and distance. Mixed effects models were run using the `lmer()` function from the `LME4` package (Bates, Machler, Bolker, & Walker, 2015) in R v. 3.5.1 (R Core Team, 2018). Degrees of freedom were estimated using Satterthwaite approximations. *p* values for type III tests were extracted using the `LMERTEST` package (Kuznetsova, Prockhoff, & Christensen, 2017). Treatment-specific slopes for distance were estimated by refitting the mixed model without main effects.

We next determined whether 3) a species' dispersal traits predicted how often a species showed evidence of spillover. To do this, we quantified “spillover occurrence” as the number of plots each of the 38 desirable species occurred in across all plots sampled from sites that showed evidence of spillover (low diversity reconstructions adjacent to remnant sources). Here we did not average across transects, but instead looked at each plot individually. We first took the log of spillover occurrence, as this transformation allowed us to maintain homogeneity of variance (tested using the `bartlett.test()` function; Bartlett's $K^2 = 0.4198$, $df = 2$, $p = .8106$). We then used ANOVAs with the `aov()` function to determine if the log of spillover occurrence was predicted by species dispersal mode including; pollen dispersal (wind or insect), seed dispersal (unassisted, wind or animal) or vegetative dispersal (none, caudex, rhizome or cespitose), classified using Cornelissen et al. (2003). We used Tukey HSD pairwise comparisons for all significant ANOVAs to determine differences between mode types using the `TukeyHSD()` function.

3 | RESULTS

We found that spillover occurred, and that species richness of reconstructions altered successful spillover. The average richness of desirable native species showed a significant three-way interaction between source type, species richness and distance ($F_{1,11.1} = 5.27$, $p = .037$, Figure 2 and Table 1). This provides evidence that the strength of spillover depends on the combination of reconstruction species richness and type of source habitat. In the low diversity, remnant-adjacent sites, we see a negative slope between desirable richness and distance up to 50 m (estimate = -0.080 , $p = .0075$). For all other sites, the slope estimates were positive and close to zero, with *p* values $0.33 \leq x \leq 0.78$. An average of 6.6 desirable species spilled

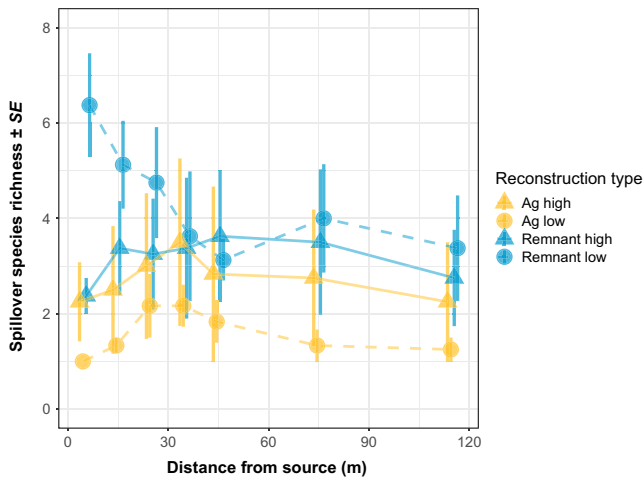


FIGURE 2 Evidence for spillover into reconstructed grasslands. We found evidence for spillover in reconstructions with low species richness adjacent to remnant grasslands (blue circles). In these sites, spillover species richness (desirable, unseeded grassland species) demonstrated a negative relationship with distance. For all other reconstructions, that is those adjacent to agricultural fields of both high and low seeded richness (yellow triangles and circles respectively), and those adjacent to remnant grasslands with high seeded richness (blue triangles), there was no distance-dependent spillover effect

TABLE 1 Statistical results for the linear mixed effects model. All effects have numerator *df* = 1, so the effect mean-square (not reported) equals the effect sum-of-squares (SS). We found a significant three-way interaction between the source habitat type (agriculture vs. remnant), reconstruction species diversity and distance from the source habitat. This indicates that the slope for the relationship between number of desirable species and distance from source depends on both the source habitat and reconstruction diversity

	SS	Den <i>df</i>	<i>F</i> value	<i>p</i> value
Source habitat	8.60	10.99	9.18	.011
Reconstruction diversity	1.97	10.99	2.10	.180
Source habitat: reconstruction diversity	7.29	10.99	7.78	.018
Distance from source	0.18	11.10	0.19	.670
Source habitat:distance from source	2.68	11.10	2.87	.120
Reconstruction diversity:distance from source	2.68	11.10	2.87	.120
Source habitat:reconstruction diversity: distance from source	5.27	11.10	5.63	.037

^aBold values correspond to statistically significant *p* < 0.05.

over at the remnant-reconstruction boundary (distance = 0 m), which is an increase of c. 230% as compared to the average richness of all other treatments (Figure 2). Desirable species richness in all treatments was an average of 2.9 species at 50 m, with no evidence

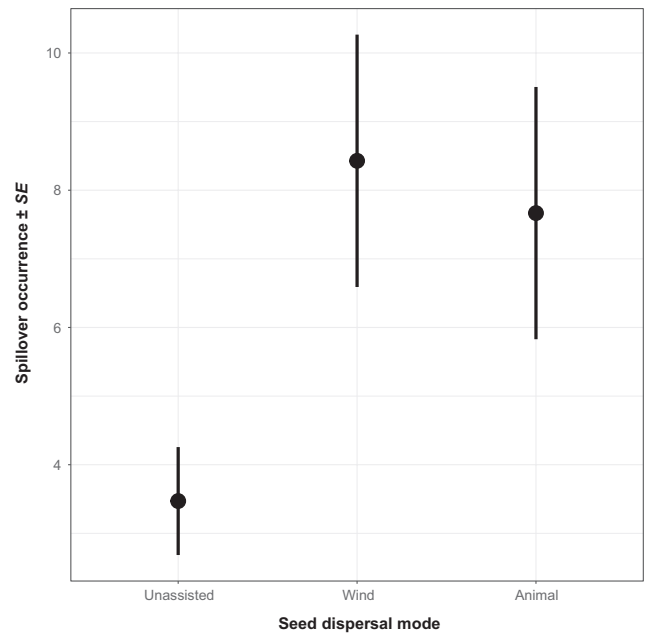


FIGURE 3 Species' seed dispersal mode predicted their spillover occurrence. Based on pairwise comparisons, species with wind dispersed seeds occurred in more plots than species with unassisted seed dispersal, whereas species with animal dispersed seeds trended towards dispersing more than those with unassisted dispersal but this was not significant. For both panels, points represent mean values and error bars represent standard error

of differences among treatments. This richness is in addition to all species in the reconstructions that were seeded or are weedy species in grasslands.

For the 38 desirable species that showed evidence of spillover (Table S1), we found that species' dispersal traits influenced the likelihood that a species would spill over. A species' seed dispersal mode ($F_{2,34} = 4.719, p = .016$), but not its pollen ($F_{1,35} = 0.000, p = .996$) or vegetative dispersal mode ($F_{3,33} = 0.374, p = .772$) significantly predicted its spillover occurrence, after removing one outlier (*Carex tetanica*). Pairwise comparison analysis revealed that spillover species with wind dispersed seeds ($p = .026$) occurred in more plots than species with unassisted dispersal. Species with animal dispersed seeds, while not significant, trended towards increased occurrence in plots as compared to unassisted dispersal ($p = .075$) (Figure 3).

4 | DISCUSSION

Our results suggest that spillover can indeed increase biodiversity in reconstructed grasslands. The species arriving via spillover were largely unique from those originally seeded to create the reconstructions. Of the 38 species that showed evidence of spillover, 71% were not included in any of the seed mixes used in the higher richness reconstructions. Because we removed seeded species from consideration for possible spillover events, a high similarity between spillover species and species included in the

high diversity seed mixes would indicate that the high richness of reconstructions masks spillover. However, we found high dissimilarity between these two sets of species, indicating that spillover provides rare species that would otherwise not be present in reconstructed grasslands. We also note that 87% of spillover species were found in their associated remnants and thus likely moved from remnant sources. That being said, spillover was not ubiquitous. Our results show that diversity increases due to spillover were contingent on both the reconstruction species richness and species' dispersal traits. We only found evidence for spillover from remnant grasslands into adjacent reconstructions with low species richness, as evidenced by the negative slope between desirable species richness and distance for such sites. This result indicates that on average, reconstructions adjacent to remnants tend to have higher spillover species richness than those adjacent to agricultural fields, that the difference in desirable species richness is largest when comparing low diversity reconstructions across source type, and that these patterns vary with distance. This results in only the lower diversity reconstructions adjacent to remnant source habitats exhibiting the negative distance-dependent relationship that characterizes spillover. We also found that plants with wind dispersed (and to some extent, animal dispersed) seeds contributed more often to spillover than plants with unassisted dispersal. Together, these results demonstrate the context dependency of spillover for promoting diversity in grasslands.

We observed evidence of rare species spillover only at sites with low richness, echoing findings from studies on invasion (e.g. Kennedy et al., 2002; Stachowicz, Whitlatch, & Osman, 1999) and colonization (Roscher, Schumacher, Gerighausen, & Schmid, 2014), where increased local richness leads to decreased establishment of novel species. Several mechanisms could cause this richness-dependent pattern. High species richness in reconstructed grasslands could mean more complete resource utilization, thus leaving little functional space in which spillover species could establish (e.g. J. Fargione et al., 2003; Mwangi et al., 2007; Tilman, 2004), a process termed "niche pre-emption" (Fukami, 2015). The observed pattern could also be explained by sampling (Wardle, 2001) or priority (Martin & Wilsey, 2012) effects, whereby early established species in high richness reconstructed grasslands are more likely to reach high abundance or large size before other species arrive, thus inhibiting recruitment of spillover species by creating unfavourable conditions. This richness-dependent pattern could be further reinforced if these mechanisms work synergistically (Fargione & Tilman, 2005). Alternatively, reconstruction practices have changed through time; seeded species richness in reconstructions has increased in Minnesota since the early 2000s, replacing the practice of seeding with many fewer species. Therefore, a third possible mechanism contributing to our observed diversity pattern could be that our older, lower richness sites had more time to accumulate species arriving via spillover. Winsa et al. (2015) found that spillover species do accumulate through time, but, similar to other studies, also found that establishment from spillover (e.g. Brudvig et al., 2009; Sullivan et al., 2018; Vespa et al., 2018; Winsa et al., 2015) or known seeding

events (e.g. Grygiel, Norland, & Biondini, 2014; Turley et al., 2017) often occurs within the first c. 5 years. This finding suggests that we ought to have seen spillover in our younger (5–10 years), high diversity sites if time was the predominant driver of spillover. That said, the relationship between time and species richness cannot be directly teased apart by our experimental design. Therefore, we encourage future work that examines the relative effects of time and diversity on spillover, as this will inform our understanding of the controls of biodiversity in reconstructed systems.

Our work also demonstrates that species' dispersal traits, specifically seed dispersal mode, play a role in the likelihood of a species spilling over into reconstructed grasslands. We found that species with wind dispersed seeds occurred in c. 142% more plots on average than those with unassisted dispersal, and wind and animal dispersal combined occurred in c. 363% more plots than those with unassisted dispersal. This result is intuitive, given that seeds with adaptations for wind (e.g. pappus, wings, etc.) and animal (e.g. fleshy fruits) dispersal often disperse farther than seeds that lack these adaptations (Matlack, 1994; Tamme et al., 2014). Indeed, other studies have found species with unassisted dispersal tend to be sensitive to fragmentation (Alados, Navarro, Komac, Pascual, & Rietkerk, 2010; Cheptou, Carrue, Rouified, & Cantarel, 2008). Our results suggest wind and animal dispersed species may be less susceptible to habitat fragmentation, as these species more successfully disperse across patch boundaries and establish in reconstructed grasslands. Additionally, because they are unlikely to arrive via spillover, species with unassisted dispersal may require targeted management efforts through assisted migration to gain a foothold in reconstructions (Vitt, Havens, Kramer, Sollenberger, & Yates, 2010). The one exception was *Carex tetanica*, which occurred in many plots, especially at one site, but has unassisted seed dispersal. A possible explanation is that *C. tetanica* is highly productive, and thus can produce enough seed to reach many plots despite having lower dispersal ability (Moles & Westoby, 2004).

Our findings have implications for managers seeking to increase diversity in grasslands. Although we found that spillover does not occur from remnants to high richness reconstructions, understanding the mechanisms behind this pattern could guide future strategies to promote spillover in higher diversity habitats. For example if the mechanism mitigating spillover is niche pre-emption, then seeded species will have a competitive advantage over subsequently arriving species within functional groups. This suggests that higher diversity reconstructions might be "stuck with what they are seeded with", and that richness could plateau at seeding. Introducing disturbances into reconstructions to create open space could allow for recruitment of new species arriving via spillover that might otherwise be out-competed due to niche pre-emption. For example grazing (Martin & Wilsey, 2006; Wilsey & Martin, 2015), as well as the combination of grazing and fire (Collins, Knapp, Briggs, Blair, & Steinauer, 1998) facilitate seedling recruitment with experimental seed additions. These disturbances could promote spillover into higher diversity reconstructions and further increase their richness.

Our results also suggest that it would be beneficial to seed high diversity seed mixes into established lower richness reconstructions. Currently, reconstructions are typically only seeded at the beginning of the reconstruction, but mimicking spillover by repeatedly seeding reconstructions could increase reconstruction species richness. However, seed additions are unlikely to exactly mimic spillover in terms of species composition, as seed mixes typically contain only a fraction of the pool of species that are considered desirable in grasslands (Ladouceur et al., 2018). In order to more realistically mimic spillover, reconstruction efforts should focus on acquiring seeds of a larger variety of species and genetic diversity (Aavik, Edwards, Holderegger, Graf, & Billeter, 2012). These limitations of contemporary seeding practices highlight some of the greatest advantages of spillover by natural dispersal: it supplies species to reconstructions that are unlikely to be included in commercially designed seed mixes and are also from nearby source populations, thereby preserving the genetic integrity of regional populations. Conversely, our results also suggest that managers should consider including species that are unlikely to arrive via spillover in seed mixes, such as species with unassisted dispersal, or those that are not found in neighbouring habitats. Future studies ought to address local issues such as seed mix composition and the frequency of its application, as well as assess how different landscape contexts, such as the relative size of remnant source habitats, affects spillover. A greater understanding of the contexts that promote or deter spillover will help to increase the area of reconstructed grasslands that can benefit from spillover's capacity to increase biodiversity.

Understanding how spillover promotes biodiversity is highly relevant given that land use changes have caused excessive biodiversity loss across ecosystems, and especially in grasslands (Newbold et al., 2016). We show that spillover can indeed increase biodiversity in degraded grasslands, but that both established diversity and species dispersal traits alter spillover. These results demonstrate that certain reconstructions and species are more likely to benefit from spillover than others, and thus additional efforts are needed to promote spillover where it is less likely to occur. Scaling our results to the state of Minnesota, we estimate that 1,258 ha of low richness reconstructed grasslands currently benefit from increased biodiversity due to spillover. This represents the total area of low richness reconstructions within 50 m of an adjacent remnant grassland that could be influenced by spillover, as this is the point where we found the effects of spillover to decrease to a minimum. This spillover could prove important for biodiversity increases, as connectivity of high-quality grassland in the region is patchy (Wimberly, Narem, Bauman, Carlson, & Ahlering, 2018). The extent to which natural spillover occurs underscores the potential impact of intentionally leveraging this process in reconstruction efforts to bolster biodiversity in these chronically species-poor systems.

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AUTHORS' CONTRIBUTIONS

K.P.S., H.H. and L.L.S. developed the ideas and collected data, L.L.S. and P.M.D. analysed the data, K.P.S. and L.L.S. wrote the manuscript, K.P.S., H.H., I.L., J.P., P.M.D. and L.L.S. edited the manuscript, and K.P.S., H.H., I.L., J.P. and L.L.S. refined the research ideas and helped with site selection.

DATA AVAILABILITY STATEMENT

Please see Appendix S1 for code description. Data are available via Zenodo <https://doi.org/10.5281/zenodo.3252034> (Sperry et al., 2019).

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