Are they two seeds in a pod? Comparing seed rain recovery using artificial grass carpets versus sticky traps in grasslands.

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ABSTRACT

Seed dispersal is a critical process for plant community assembly, however natural rates of seed arrival are rarely quantified when compared to other assembly mechanisms, especially in herbaceous communities. This discrepancy arises from the difficulty in recovering small seeds. Here we compare the utility of artificial grass carpet squares ('artificial grass') for capturing seed rain to classic 'sticky trap' methods. While artificial grass has been used in Arctic systems, we examine its efficacy in temperate grasslands. We placed paired sticky traps and artificial grass squares in two grassland ecosystems. We added known numbers of seeds of multiple species to each trap, and recovered seeds at one week, one month and two month intervals. We found that while both trap types lost seeds through time at similar rates, sticky traps recovered more small seeds while artificial grass recovered more large seeds. Overall sticky traps retained more seeds, but recovering seeds was difficult, and recovery was hindered by debris stuck to the traps. Alternatively, seeds recovered from artificial grass could be handled easily and retained for long-term storage. We encourage artificial grass traps for broad adoption of measuring seed rain in grasslands to increase links between theoretical and empirical community ecology.

INTRODUCTION

Dispersal is a critical process that structures populations and communities, linking local patch-scale dynamics to regional landscape level processes (Amarasekare, 2003; Snyder & Chesson, 2003; Leibold & Chase, 2017). Within vegetative communities, seed dispersal is one of the primary mechanisms of arrival to new habitats, allowing species to track changing environmental conditions and promoting landscape connectivity (Cubiña & Aide, 2001; Simberloff, 2009; Beckman & Sullivan, 2023). Dispersal also plays a critical role in assembly and long-term diversity patterns, such as maintaining source-sink dynamics (Mouquet & Loreau, 2003; Craig *et al.*, 2025), allowing long-term species co-existence (Snyder & Chesson, 2003; Berkley *et al.*, 2010), and maintaining genetic diversity in populations (Jordano, 2017). A species' dispersal ability also has direct management implications, often increasing native diversity after restoration, or alternatively, facilitating the invasion of non-native species (Von Der Lippe & Kowarik, 2007; Sperry *et al.*, 2019; Brudvig *et al.*, 2009). Despite its importance as a critical process for populations and communities (Vellend, 2010; Schupp & Fuentes, 1995; Levine & Murrell, 2003), dispersal is notoriously difficult to quantify empirically (Beckman & Sullivan, 2023; Bullock *et al.*, 2006). These methodological challenges have created a gap between our theoretical understanding of the importance of dispersal versus our empirical understanding and use in applied settings (Bolker *et al.*, 2003), making dispersal arguably the least empirically understood mechanism of community assembly (HilleRisLambers *et al.*, 2012; Vellend, 2016).

One way to measure seed dispersal is by estimating seed rain, or the seeds that fall into a given area (Arruda *et al.*, 2018a). While this method captures only a single point in the dispersal trajectory of a seed (the settlement phase - Travis *et al.* 2012), it is arguably the most important phase to understand for plant community ecology, as it provides information on the number and type of seeds that arrive to a specific location. If seeds are recovered before post-dispersal seed predation or secondary dispersal occurs, then this is considered a measure of *primary dispersal*. However, if seeds that fall to a given area are then lost to these processes this measure of seed arrival is considered to be *effective dispersal* as it constitutes the seeds that have a chance to germinate and establish in a given area (Nathan & Muller-Landau, 2000). Quantifying seed rain as a measure of seed arrival across many different natural environments is critical for building strong links between plant community ecology experiments and theory (Myers & Harms, 2009).

Seed rain is typically measured through the use of seed traps placed on or near the ground in an ecosystem of interest (Cottrell, 2004; Kollmann & Goetze, 1998). Seed traps are commonly used in forest systems to measure seed rain (Cottrell, 2004; Rogers *et al.*, 2017; Huanca Nuñez *et al.*, 2021; Piotto *et al.*, 2019), and when there are known parents, dispersal trajectories can be calculated using inverse modeling (Wälder *et al.*, 2009; Nathan & Muller-Landau, 2000). Seed rain measurements, however, are much less common in ecosystems with predominently herbaceous communities (e.g. grasslands, tundra), with only a handful of studies estimating seed rain in grasslands specifically (Rabinowitz & Rapp, 1980; West & Durham, 1991; Schott & Hamburg, 1997; Kettenring & Galatowitsch, 2011; Willand *et al.*, 2015; Wynne *et al.*, 2024). This dearth of knowledge on herbaceous seed rain likely occurs because recovering small herbaceous seeds is challenging (Myers & Harms, 2009) and seed identification resources for even common species' can be scarce (Wynne *et al.*, 2024). The main method for capturing seed rain in grasslands is via sticky traps, where a flat surface (often a petri dish) is sprayed with a sticky substance, and seeds that falls onto the surface are captured and later recorded (Rabinowitz & Rapp, 1980). Sticky traps present multiple practical problems, including that they have to be replaced frequently because the sticky surface can become completely covered in leaves and debris, thereby blocking newly fallen seeds from capture. Furthermore, sticky traps are no longer sticky once temperatures fall below freezing, despite this being a critical time for seed dispersal in temperate grasslands

(Rabinowitz & Rapp, 1980). Lastly, using recovered seeds from sticky traps for additional work, such as germination trials or trait measurement, is rarely possible as seeds become coated with the sticky residue.

An alternative method for measuring seed rain is to use artificial grass carpets. With this method, artificial grass patches are fixed to the ground, seeds are dispersed into traps, and they are caught in artificial grass strands. This method is used to sample seed rain in the Arctic (Molau, 1996; Molau & Larsson, 2000), and provides a potential solution to the many issues that arise with collecting seed rain via sticky traps in grasslands more generally. Artificial grass can remain in the field for long periods of time and still capture seeds, withstand large temperature and hydrologic fluctuations, and collected seeds can be germinated after capture should visual identification not be possible due to lack of seed identification resources (Wolters *et al.*, 2004; Molau, 1996). These features make artificial grass carpets a viable option for seed rain studies in grasslands. For example, recently Wynne et al. 2024 used artificial grass carpets for capturing seed rain in a successional chronosequence of temperate tallgrass prairies and were able to recover ∼27,000-124,000 seeds per square meter depending on the age of the grassland. Although the artificial grass carpet method appears promising for widespread use for collecting seed rain in grasslands, we currently lack a comparison between this and the sticky trap method to compare their ability to recover seeds and to consider potential biases across methods.

Here, we investigate the effectiveness of traditional sticky traps (Tangle-Trap® resin on Plexiglass® Petri plates) as compared to artificial grass traps for measuring seed rain in grasslands. We examined the seed retention efficacy of both methods through time, comparing the proportion of seeds recovered across two temperate grassland ecosystems, a diversity of species, and a range of seed sizes. While traditional sticky traps had a higher recovery rate of smaller seeds, both methods recovered a high proportion of seeds overall, and seeds from artificial turf traps were in better condition for counting, identification, and post-processing measurements. As such, we suggest that artificial turf traps be used for measuring seed rain in grassland communities, especially when it may be beneficial to germinate collected seeds or in remote locations where it is difficult to replace traps frequently (Rabinowitz & Rapp, 1980; Cottrell, 2004). By having robust comparisons of different seed rain capture methods, we can better advance our empirical understanding of dispersal, thus narrowing the current gap between theory and data, and advancing our understanding of the role of dispersal in grassland restoration and conservation.

METHODS

Study sites and seed mixes

We replicated experimental tests of seed capture methods for detecting seed rain in two distinct grassland communities: a shortgrass prairie in northern Colorado, and a tallgrass prairie in central Missouri (Fig. 1A, B).

The Colorado (CO) study occurred on private land bordering the Cathy Fromme Prairie Open Space, a 267 ha remnant of native shortgrass prairie. The site is relatively flat, surrounded by mature cottonwood trees, and receives approximately 38 cm of precipitation annually (Balok *et al.*, 1995).

The Missouri (MO) study occurred on a restored tallgrass prairie owned by the University of Missouri. The prairie was located on campus, and is surrounded by buildings and foot-traffic, and receives approximately 108 cm of annual precipitation (Gu *et al.*, 2015).

Experimental design and tests of trap performance

We tested the effectiveness of sticky traps versus artificial grass carpets for seed retention through time. Following standard protocol (Rabinowitz & Rapp, 1980; Kollmann & Goetze, 1998; Chabrerie & Alard, 2005), sticky traps consisted of 10 cm x 10 cm Plexiglass plates coated with Tangle-Trap® sticky coating. To compare this standard method to seed carpets, we used 10 cm x 10 cm synthetic lawn turf squares (TrafficMASTER® TruGrass Emerald Artificial Turf) with blade heights between 1.5 to 2.5 cm tall.

At the two sites, we replicated 10 blocks of paired sticky traps and carpets that we collected 1 week, 1 month, and 2 months after deployment to examine seed recovery through time. We initially deployed all traps on July 10, 2019 in Colorado and July 17, 2019 in Missouri. Each block consisted of three sticky traps and three carpets for a total of 10 replicates of the two methods for each each time point and each site. When deploying traps, we removed any litter or vegetation directly under the traps so that they were placed directly on the soil surrounded by natural vegetation (Fig. 1E). We used two ground staples to secure opposite sides of each trap. On each trap, we then placed 20 seeds of 8 locally occurring species, where seed mixes were chosen such that they encompassed a range of functional groups and seed mass (see Table 1 for species and associated seed mass, Fig. 1C, D). At the Colorado site, we used only 10 seeds for the species at the highest end our seed mass range, *Yucca glauca*, due to their large size, resulting in a total of 150 (CO) and 160 (MO) seeds per trap.

We collected paired sticky traps and carpets 1 week, 1 month, and 2 months after deployment. All traps were taken back to the lab for processing. We recorded the total number of seeds of each focal species that were recaptured on each trap, and noted if seed fragments were evident to suggest seed herbivory or animal activity.

At the Missouri site, we also wanted to test the efficacy of the sticky traps after they had been in the field for some time and accumulated leaves and other debris. Therefore, at the initial trap deployment date, we placed an additional sticky trap at each block that was coated in Tangle-Trap®, but did not have the seed mix added initially. After one month of sitting in the grassland and accumulating leaves and other debris naturally, we added the same seed mix as above to these traps, and then collected these traps along with the two-month traps. We termed this treatment, the 'post-sticky' treatment. We recovered and identified seeds from these traps in the same manner as mentioned above. This allowed us to more closely examine how well sticky traps recovered seeds after longer periods of time in the field.

Statistical analysis

To visualize how relative seed recovery varied across species and trap type, we calculated log response ratios of seed recovery of sticky traps relative to artificial grass carpet traps for each species at each site (i.e. the log of % recovery on sticky traps divided by % recovery on artificial grass traps). For this formulation, values greater than zero indicate seeds are more likely to be recovered on sticky traps, values of less than zero are more likely to be recovered on carpets, and values of zero indicate seeds are equally likely to be recovered on both traps. This allows for ease of visualization of which trap type tends to recover relatively more seeds of a given species at a given time.

To determine how absolute seed recovery depended on the trap type, seed mass and the amount of time the traps remained in the field, we used generalized linear mixed effects models using the 'glmmTMB' package (Brooks *et al.*, 2017) in R v4.3.3. (R Core Team, 2024). The percent of recovered seeds was our response variable, and accordingly we used a binomial model with weights specified as the number of seeds placed on the traps to account for differing numbers of seeds per species used in the experiment. Our predictor variables included the interaction of trap type, seed mass and time in the field. We also included an additive random intercept for block nested within site (MO or CO). We used a backward selection approach to determine which interactions we kept in the model, and removed non-significant interactions when they arose. We calculated contrasts between trap type predictions for given seed masses using 'emmeans' (Lenth, 2023).

To determine how well the sticky traps recovered seeds once the traps had been in the field for some time and acquired debris, we explored how recovery differed between the post-sticky treatment and the other trap types that contained seeds for one month. At the Missouri site only, we subset our data to all traps that had seeds on them for one month (artificial grass, sticky and post-sticky). We then ran a similar generalized linear mixed effects model as above, with our response variable as the proportion of seeds recovered (modeled as a binomial distribution), our predictor variable as trap type, and two additive random intercepts, one for block and one for species. We then calculated contrasts with 'emmeans' between trap type.

We wrangled and visualized data with the 'tidyverse' package (Wickham *et al.*, 2019), and ran all code in R Studio v2024.12.0+467 (Posit team, 2024).

RESULTS

Relative seed recovery varied by species and time (Fig. 2). We observed that some species were more likely to be recovered on sticky traps (positive log response ratio, e.g. *C. tinctoria, D. purpurea*), others were more likely to be recovered on artificial grass traps (negative log response ratio, e.g. *H. annuus, S. heterolepis*), and many were equally likely to be recovered on either trap type (e.g. *S. scoparium, B. dactyloides*). These trends often varied with time.

We next explored how trap type, seed mass, and the time the traps spent in the field altered the absolute proportion of seeds recovered. We found a significant interaction between seed mass and trap type, and a significant additive effect of time (Table 2). On average, sticky traps recovered more seeds than artificial grass traps, with sticky traps recovering $\sim 74\% \pm 13\%$ of seeds, and artificial grass traps recovering $\sim 52\% \pm 18\%$ of seeds. However, this relationship depended on seed mass (Fig. 3). As seed mass increased, the proportion of seeds recovered increased on artificial grass carpets, but decreased on sticky traps. For small seed masses, artificial grass traps caught significantly fewer seeds (log odds estimate at seed mass of 0, estimate= -1.56 ± 0.04 SE, $p < 0.001$). However, at large seed sizes, artificial grass traps caught significantly more seeds (log odds estimate at seed mass of 0.02, estimate= 0.75 ± 0.13 SE, $p < 0.001$). Additionally, the longer the traps were in the field, the more seeds were lost (Supplemental Information). Across both trap types, $\sim 30\%$ seeds were lost for each month the traps spent in the field.

Finally, to determine how well the sticky traps continue to capture seeds after some time in the field, we conducted the 'post-sticky' trial at the Missouri site. We found that sticky traps caught a significantly larger proportion of seeds than the post-sticky treatment, but there was no difference found between the seeds captured with the aritifical grass and the post-sticky treatments (Fig. 4, Table 3). The post-sticky traps captured $\sim 30\%$ less seeds than the sticky traps.

DISCUSSION

A broader understanding of the natural rates of seed rain in grasslands is necessary to understand the role of seed arrival for the assembly and reassembly of plant communities under global change (Myers & Harms, 2009; Arruda *et al.*, 2018b). Standardized methods for estimating seed arrival and dispersal dynamics that are flexible and can adequately recover seeds under a myriad of conditions is critical, given that grasslands span $\sim 40\%$ of the Earth's surface, and occur on all continents across a wide range of precipitation and temperature regimes (Buisson *et al.*, 2022). Here we provide a test of the seed recovery efficacy of two methods for measuring seed rain in grassland communities: artificial grass traps and sticky traps. These methods are both easy to deploy because of their size and minimal impact on the local community (as compared to other funnel or pitfall-based methods; Kollmann & Goetze, 1998). While both methods are successful for recovering seeds, our experimental comparison has led us to encourage the use of artificial grass traps for capturing seed rain in grasslands, especially for seeds that are larger in mass, for the reasons we describe below. Obtaining estimates of local dispersal across a range of grassland communities will help bridge the gap between dispersal theory and empiricism (Bolker *et al.*, 2003; Amarasekare, 2003; Myers & Harms, 2009).

We find that both the artificial grass and sticky trap methods have high rates of seed recovery (72% for sticky traps on average, compared to 52% for artificial grass traps), with decreasing recovery through time. Seed loss from both trap types was due to both abiotic and biotic reasons, such as strong rainfall events washing seeds off carpets or herbivory of seeds. In our study, we found evidence for both scenarios; for example a large, single-day rainfall event decreased seed recovery at the Colorado site between time point 1 (1 week after deployment) and time point 2 (1 month after deployment). Evidence of both insect and small mammal herbivory occurred across both sites, with hundreds of ants on some sticky traps (Fig. 1G), cottontail rabbit (*Sylvilagus sp.*) feces on seed carpets (Fig. 1F), and husks of seeds post-consumption were found on both trap types, especially after longer periods of time. These findings indicate that no trap type is a perfect representation of primary dispersal, but instead represents a measure of *effective dispersal* (Nathan & Muller-Landau, 2000), where recovered seeds are those that have escaped herbivory or secondary dispersal and could germinate and join the aboveground community. Therefore, the artificial grass trap method arguably represents more "ecologically relevant dispersal" for the local community, because the traps allow for seed loss that would occur naturally on the soil surface - leading to recovered seeds being those that have the potential to germinate. We suggest future studies examine herbivory rates on seed carpets, deploying paired carpets in herbivory removal and control plots. Seed carpet methods could be extended from our current focus on seed rain to examine herbivory rates or even conduct preference experiments in grasslands (Edwards & Crawley, 1999; Bakker & Olff, 2003).

While sticky traps are more commonly used in field studies (e.g. Rabinowitz & Rapp, 1980) and retain more seeds on average, they also have many drawbacks for accurately measuring seed rain. Sticky traps capture everything that comes in contact with the surface of the Petri dish (Fig. 1G), and thus sorting seeds from plant and soil debris as well as insect bodies can be difficult. Recovery is especially difficult for small seeds that have the potential to stick to debris in the trap and be easily missed. In our work we were focused on finding a known set of species. However, once the identity of seeds are unknown (as in classic seed rain studies, compared to our comparative methods-focused approach), the ability to lose seeds due to accidentally sticking to other material will decrease seed recovery. We also noticed that some species with thinner seed coats changed color after being in contact with Tangle-Trap® for long periods of time, which can hinder identification if seeds are not removed and identified quickly. Given how time-consuming seed removal and identification can be (Wynne *et al.*, 2024), it is critical to have a method that allows samples to be stored for long periods and remain unaffected. In addition, it is nearly impossible to recover seeds from sticky traps and then germinate them to determine viability or identity, whereas this is quite simple with artificial grass carpets. The potential to germinate 'unknowns' is, in our view, a key advantage of artificial grass traps, given unknowns are extremely likely in seed rain studies (Wynne *et al.*, 2024). Finally, the timing of sticky traps is extremely important for their effectiveness. Sticky traps no longer capture seeds effectively once they have been frozen (Molau, 1996), which makes post-frost seed rain collection impossible despite many temperate seeds dispersing late in the growing season or under snowy conditions (Rabinowitz & Rapp, 1980; Molau & Larsson, 2000). In addition, our results from the Missouri site clearly show that sticky traps work best when they are in the field for short periods of time, or else debris collects on the trap and hinders seed capture and recovery (Fig. 4). This is in comparison to artificial grass traps that continue to effectively collect and store seeds regardless of time or temperature. Our work strongly supports the use of artificial grass traps as a primary method to measure seed rain in grasslands because these traps improve the ease of identifying unknown seeds, and can successfully recover seeds under many different site conditions and time-scales.

Our results demonstrated that the relationship between seed mass and seed recovery changes with trap type (Fig. 3). As seed size increases, we see a small decrease in the proportion of seeds recovered on sticky traps, but a large increase in the proportion of seeds recovered on artificial grass traps. This result likely arises from differences in the body size of the granivores consuming seeds from the traps. Broadly, there is a positive relationship between granivore body size and the size of seeds they consume (Muñoz & Bonal, 2008), with smaller-bodied insect granivores tending to favor smaller seeds than larger-bodied small mammal granviores (Radtke, 2011; Maron *et al.*, 2012; Rey *et al.*, 2002; Vaz Ferreira *et al.*, 2011). The loss of smaller seeds from the artificial grass traps likely reflects how well the Tangle-Trap® captures insects like ants that attempt to remove seeds from these traps, but instead become stuck to the surface of the sticky trap (Fig. 1G). Therefore, more smaller seeds remain to be recaptured on the sticky traps because insect granivores are not removing them. Conversely, larger seeds ar emore likely to be recovered on the artificial grass traps. Here, larger seeds are likely consumed by small mammals, and are likely easier to consume from sticky traps because they are fixed on the soil surface and not hidden among the strands of grass as they are in the artificial grass traps. This decrease in handling time could increase consumption rates of larger seeds from sticky traps. While the exact reason for why we find this interaction between trap type and seed mass should be further explored, this result underscores the importance of considering the difference in the results provided by the different trap methods. If the goal is to understand primary seed dispersal and to quantify the number and type of seeds that fall regardless of their fate, we encourage the use of sticky traps that are replaced very frequently (and of course considering all possible concerns listed above). However if the goal is to understand 'effective dispersal', which focuses more on which seeds remain in an area and are available to germinate and establish into the vegetative community, we encourage the use of artificial grass traps because they allow natural processes such as secondary dispersal and granivory to occur.

Here we present a methodological comparison between the seed recovery ability of artificial grass traps and sticky traps for measuring seed rain in grasslands. While we find both methods effectively recover seeds, overall this comparison underscored that artificial grass traps are much simpler and less hassle to use. Artificial grass traps are effective at seed recovery under a wider range of conditions, and allow for future, downstream use of seeds once the traps have been removed from the field. This method will allow for coordinated understanding of seed rain across grasslands (Arruda *et al.*, 2018b; Myers & Harms, 2009). Future seed rain studies will do well to consider the time they leave the traps out in the field, as seeds tend to be increasingly lost through time. This seed loss is inevitable, and represents the fates of seeds on the soil surface (Forget *et al.*, 2005; Chambers & Macmahon, 1994), as small mammals and insects consume many seeds in grasslands throughout the season (Howe *et al.*, 2002; Peters, 2007; Kuli-Révész *et al.*, 2021).

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Author Contributions

LLS and LGS designed and implemented experiment, conducted statistical analysis, and wrote the manuscript, all authors helped with data collection and manuscript editing.

Data Availability

Code and data for analysis and figure generation can be found at Github (`https://github.com/Sullivan-Lab/project$_$CarpetMethods`), and will be made available at Dryad upon publication.

References

Amarasekare, P. (2003). Competitive coexistence in spatially structured environments: a synthesis. *Ecology letters*, 6, 1109–1122.

Arruda, A. J., Buisson, E., Poschlod, P. & Silveira, F. A. O. (2018a). How have we studied seed rain in grasslands and what do we need to improve for better restoration? *Restoration Ecology*, 26.

Arruda, A. J., Buisson, E., Poschlod, P. & Silveira, F. A. O. (2018b). How have we studied seed rain in grasslands and what do we need to improve for better restoration? *Restoration Ecology*, 26.

Bakker, E. S. & Olff, H. (2003). Impact of different-sized herbivores on recruitment opportunities for subordinate herbs in grasslands. *Journal of Vegetation science*, 14, 465–474.

Balok, R., Albers, R., Manci, K., McBride, K., Miller, J., Mosnik, D., Taylor, V. & Zentz, R. (1995). Cathy fromme prairie site management plan. *Natural Resources Department, City of Fort Collins, Colorado.*

Beckman, N. G. & Sullivan, L. L. (2023). The Causes and Consequences of Seed Dispersal. *Annu. Rev. Ecol. Evol. Syst. 2023*, 54, 2023.

Berkley, H. A., Kendall, B. E., Mitarai, S. & Siegel, D. A. (2010). Turbulent dispersal promotes species coexistence. *Ecology Letters*, 13, 360–371.

Bolker, B. M., Pacala, S. W. & Neuhauser, C. (2003). Spatial dynamics in model plant communities: what do we really know? *The American Naturalist*, 162, 135–148.

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M. & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9, 378–400.

Brudvig, L. A., Damschen, E. I., Tewksbury, J. J., Haddad, N. M. & Levey, D. J. (2009). Landscape connectivity promotes plant biodiversity spillover into non-target habitats. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 9328–32.

Buisson, E., Archibald, S., Fidelis, A. & Suding, K. N. (2022). Ancient grasslands guide ambitious goals in grassland restoration. *Science*, 377, 594–598.

Bullock, J. M., Shea, K. & Skarpaas, O. (2006). Measuring plant dispersal: an introduction to field methods and experimental design. *Plant Ecology*, 186, 217–234.

Chabrerie, O. & Alard, D. (2005). Comparison of three seed trap types in a chalk grassland: toward a standardised protocol. *Plant Ecology*, 176, 101–112.

Chambers, J. C. & Macmahon, J. A. (1994). A day in the life of a seed: Movements and fates of seeds and their implications for natural and managed systems. *Annual Review of Ecology and Systematics*, 25, 263–292.

Cottrell, T. R. (2004). Seed rain traps for forest lands: Considerations for trap construction and study design. *BC Journal of Ecosystems and Management*, 5, 1–6.

Craig, E. F., Szojka, M., Germain, R. M. & Shoemaker, L. G. (2025). Species occupancy is inflated by sink populations in productive environments but not unproductive environments. *Ecology*, 106, e70089.

Cubiña, A. & Aide, T. M. (2001). The effect of distance from forest edge on seed rain and soil seed bank in a tropical pasture 1. *Biotropica*, 33, 260–267.

Edwards, G. & Crawley, M. (1999). Herbivores, seed banks and seedling recruitment in mesic grassland. *Journal of Ecology*, 87, 423–435.

Forget, P. M., Lambert, J. E., Hulme, P. E. & Vander Wall, S. B., eds. (2005). *Seed Fate: Predation, Dispersal and Seedling Establishment*. CABI Publishing, Cambridge.

Gu, L., Pallardy, S. G., Hosman, K. P. & Sun, Y. (2015). Drought-influenced mortality of tree species with different predawn water dynamics in a decade-long study of a central us forest. *Biogeosciences*, 12, 2831–2845.

HilleRisLambers, J., Adler, P. B., Harpole, W. S., Levine, J. M. & Mayfield, M. M. (2012). Rethinking community assembly through the lens of coexistence theory. *Annual review of ecology, evolution, and systematics*, 43, 227–248.

Howe, H. G., Brown, J. S. & Zorn-Arnold, B. (2002). A rodent plague on prairie diversity. *Ecology Letters*, 5, 30–36.

Huanca Nuñez, N., Chazdon, R. L. & Russo, S. E. (2021). Seed-rain–successional feedbacks in wet tropical forests. *Ecology*, 102, e03362.

Jordano, P. (2017). What is long-distance dispersal? And a taxonomy of dispersal events. *Journal of Ecology*, 105, 75–84.

Kettenring, K. M. & Galatowitsch, S. M. (2011). Seed Rain of Restored and Natural Prairie Wetlands. *Wetlands*, 31, 283–294.

Kollmann, J. & Goetze, D. (1998). Notes on seed traps in terrestrial plant communities. *Flora*, 193, 31–40.

Kuli-Révész, K., Korányi, D., Lakatos, T., Szabó, R., Batáry, P. & Gallé, R. (2021). Smaller and Isolated Grassland Fragments Are Exposed to Stronger Seed and Insect Predation in Habitat Edges. *Forests*, 12, 54.

Leibold, M. A. & Chase, J. M. (2017). *Metacommunity Ecology, Volume 59*. Princeton University Press.

Lenth, R. V. (2023). *emmeans: Estimated Marginal Means, aka Least-Squares Means*. URL `https://CRAN.R-project.org/package=emmeans`. R package version 1.8.4-1.

Levine, J. M. & Murrell, D. J. (2003). The community-level consequences of seed dispersal patterns. *Annual Review of Ecology, Evolution, and Systematics*, 34, 549–574.

Maron, J. L., Pearson, D. E., Potter, T. & Ortega, Y. K. (2012). Seed size and provenance mediate the joint effects of disturbance and seed predation on community assembly. *Journal of Ecology*, 100, 1492–1500.

Molau, U. (1996). Seed rain monitoring at ITEX sites. In: *ITEX Manual* (eds. Molau, U. & Molgaard, P.). p. 42.

Molau, U. & Larsson, E.-L. (2000). Seed rain and seed bank along an alpine altitudinal gradient in Swedish Lapland. *Canadian Journal of Botany*, 78, 728–747.

Mouquet, N. & Loreau, M. (2003). Community patterns in source-sink metacommunities. *The american naturalist*, 162, 544–557.

Muñoz, A. & Bonal, R. (2008). Are you strong enough to carry that seed? Seed size/body size ratios influence seed choices by rodents. *Animal Behaviour*, 76, 709–715.

Myers, J. A. & Harms, K. E. (2009). Seed arrival, ecological filters, and plant species richness: A meta-analysis. *Ecology Letters*, 12, 1250–1260.

Nathan, R. & Muller-Landau, H. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, 15, 278–285.

Peters, H. A. (2007). The significance of small herbivores in structuring annual grassland. *Journal of Vegetation Science*, 18, 175–182.

Piotto, D., Craven, D., Montagnini, F., Ashton, M., Oliver, C. & Thomas, W. W. (2019). Successional, spatial, and seasonal changes in seed rain in the Atlantic forest of southern Bahia, Brazil. *PLOS ONE*, 14, e0226474.

Posit team (2024). *RStudio: Integrated Development Environment for R*. Posit Software, PBC, Boston, MA. URL `http://www.posit.co/`.

R Core Team (2024). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. URL `https://www.R-project.org/`.

Rabinowitz, D. & Rapp, J. K. (1980). Seed rain in a North American tall grass prairie. *Journal of Applied Ecology*, 17, 793–802.

Radtke, T. M. (2011). Granivore seed-size preferences. *Seed Science Research*, 21, 81–83.

Rey, P. J., Garrido, J. L., Alcántara, J. M., Ramírez, J. M., Aguilera, A., García, L., Manzaneda, A. J. & Fernández, R. (2002). Spatial variation in ant and rodent post-dispersal predation of vertebrate-dispersed seeds. *Functional Ecology*, 16, 773–781.

Rogers, H. S., Buhle, E. R., HilleRisLambers, J., Fricke, E. C., Miller, R. H. & Tewksbury, J. J. (2017). Effects of an invasive predator cascade to plants via mutualism disruption. *Nature Communications*, 8, 6–13.

Schott, G. W. & Hamburg, S. P. (1997). The seed rain and seed bank of an adjacent native tallgrass prairie and old field. *Canadian Journal of Botany*, 75, 1–7.

Schupp, E. W. & Fuentes, M. (1995). Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience*, 2, 267–275.

Simberloff, D. (2009). The role of propagule pressure in biological invasions. *Annual Review of Ecology, Evolution, and Systematics*, 40, 81–102.

Snyder, R. E. & Chesson, P. (2003). Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. *Ecology letters*, 6, 301–309.

Sperry, K. P., Hilfer, H., Lane, I., Petersen, J., Dixon, P. M. & Sullivan, L. L. (2019). Species diversity and dispersal traits alter biodiversity spillover in reconstructed grasslands. *Journal of Applied Ecology*, 56, 2216–2224.

Travis, J. M., Mustin, K., Bartoń, K. A., Benton, T. G., Clobert, J., Delgado, M. M., Dytham, C., Hovestadt, T., Palmer, S. C., Van Dyck, H. & Bonte, D. (2012). Modelling dispersal: An eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. *Methods in Ecology and Evolution*, 3, 628–641.

Vaz Ferreira, A., Bruna, E. M. & Vasconcelos, H. L. (2011). Seed predators limit plant recruitment in Neotropical savannas. *Oikos*, 120, 1013–1022.

Vellend, M. (2010). Conceptual synthesis in community ecology. *The Quarterly Review of Biology*, 85, 183–206.

Vellend, M. (2016). The theory of ecological communities (mpb-57). In: *The theory of ecological communities (MPB-57)*. Princeton University Press.

Von Der Lippe, M. & Kowarik, I. (2007). Long-distance dispersal of plants by vehicles as a driver of plant invasions. *Conservation Biology*, 21, 986–996.

West, N. E. & Durham, S. (1991). Seed Rain On and Near a Coal Stripmine in Southwestern Wyoming. *Proceedings of the American Society of Mining and Reclamation*, 573–582.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache, S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K. & Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, 4, 1686.

Willand, J. E., Baer, S. G. & Gibson, D. J. (2015). Propagule abundance and richness are equivalent or higher in communities restored with local ecotypes relative to cultivars of dominant species. *Journal of Vegetation Science*, 26, 421–430.

Wolters, M., Geertsema, J., Chang, E. R., Veeneklaas, R. M., Carey, P. D. & Bakker, J. P. (2004). Astroturf seed traps for studying hydrochory. *Functional Ecology*, 18, 141–147.

Wynne, K. C., Parker-Smith, M. J., Murdock, E. M. & Sullivan, L. L. (2024). Quantifying seed rain patterns in a remnant and a chronosequence of restored tallgrass prairies in north central Missouri. *Journal of Applied Ecology*, 61, 3017–3027.

Wälder, K., Näther, W. & Wagner, S. (2009). Improving inverse model fitting in trees—Anisotropy, multiplicative effects, and Bayes estimation. *Ecological Modelling*, 220, 1044–1053.

Site	Family	Species	Seed Mass (mg)
Colorado	Fabaceae	*Amorpha fruticosa*	7.543 (± 0.243)
	Poaceae	*Bouteloua gracilis*	0.540 (± 0.073)
	Poaceae	*Buchloe dactyloides*	11.785 (± 0.555)
	Fabaceae	*Dalea purpurea*	1.545 (± 0.060)
	Asteraceae	*Helianthus annuus*	6.750 (± 0.330)
	Asteraceae	*Solidago rigida*	0.759 (± 0.025)
	Iridaceae	*Sisyrinchium angustifolium*	0.840 (± 0.044)
	Agavaceae	*Yucca glauca*	19.902 (± 0.518)
Missouri	Asteraceae	*Coreopsis tinctoria*	0.215 (± 0.014)
	Fabaceae	*Desmodium canadense*	4.420 (± 0.302)
	Asteraceae	*Echinacea pallida*	4.600 (± 0.183)
	Fabaceae	*Lespedeza capitata*	3.280 (± 0.099)
	Asteraceae	*Rudbeckia hirta*	0.250 (± 0.010)
	Poaceae	*Schizachyrium scoparium*	1.830 (± 0.114)
	Poaceae	*Sporobolus heterolepis*	2.000 (± 0.087)
	Campanulaceae	*Triodanis perfoliata*	0.025 (± 0.002)

Table 1: A list of all species used in the experiments in Colorado (CO) and Missouri (MO). Seed mass is measured in milligrams and reported as mean and standard deviation.

	Estimate	St. Error	z value	p value
Intercept(artificial grass)	0.589	0.185	3.18	0.001
trap type(sticky)	1.558	0.044	35.24	<0.0001
seed mass	102.518	5.683	18.04	<0.0001
time	-0.857	0.024	-36.24	<0.0001
trap type(sticky):seed mass	-115.204	7.667	-15.03	<0.0001

Table 2: Summary table of our statistical model results from our generalized linear mixed effects model exploring how trap type, seed mass and time since deployment alters the proportion of seeds recovered.

	Estimate	St. Error	z value	p value
Intercept(post-sticky)	0.152	0.286	0.53	0.596
artificial grass	0.166	0.33	0.507	0.612
sticky	1.647	0.394	4.18	<0.0001

Table 3: Summary table from our statistical model results from our 'post-sticky' analysis using a generalized linear mixed effects model exploring how trap type (post-sticky, vs artificial grass vs sticky) alters the proportion of seeds recovered.

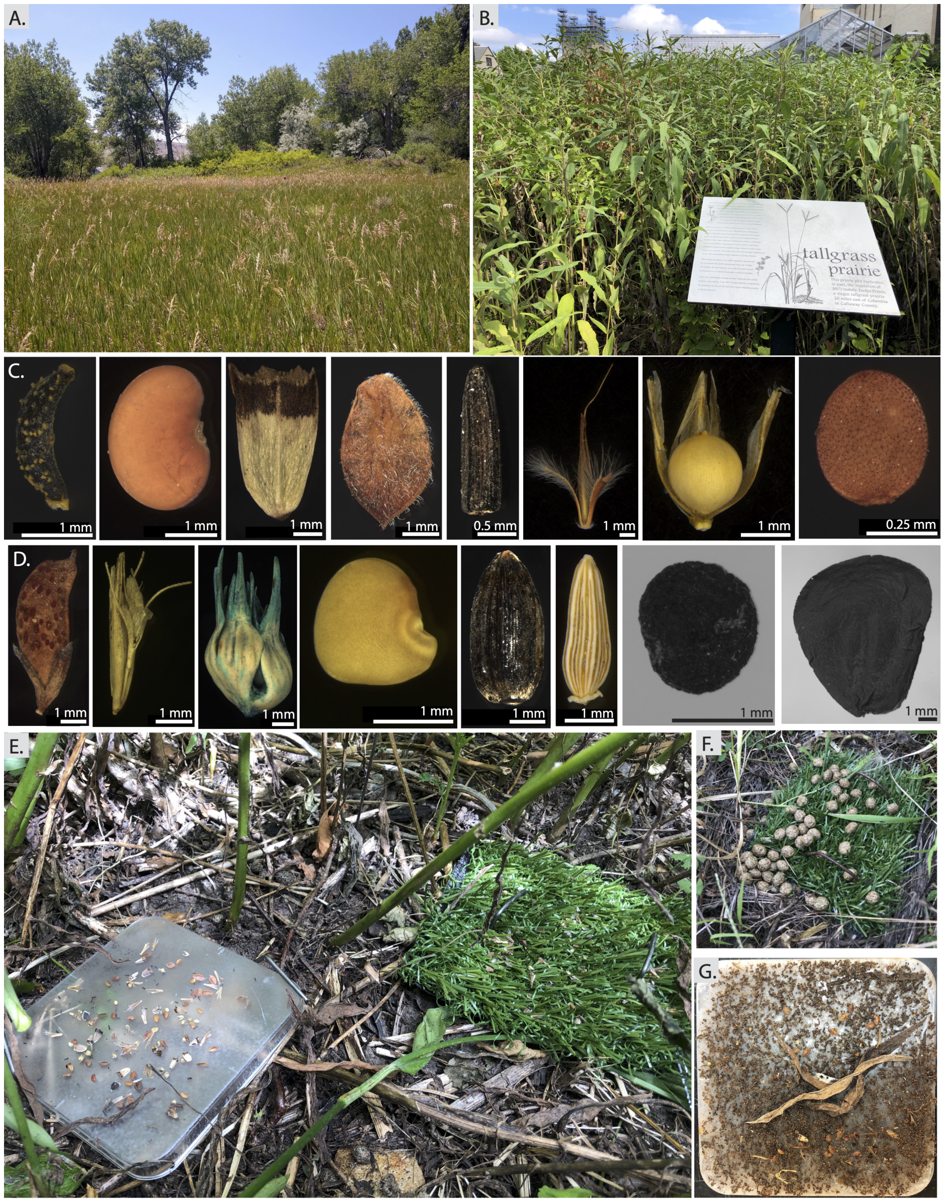

Figure 1: Depiction of our experimental sites, seeds, and methods. A) The Colorado grassland site. B) The Missouri grassland site. C) Missouri seeds used in the experiment (from left to right: *Coreposis tinctoria, Desmodium canadense, Echinacea pallida, Lespedeza capitata, Rudbeckia hirta, Schizachyrium scoparium, Sporobolus heterolepis, Triodanis perfoliata*). D) Colorado seeds used in the experiment (from left to right: *Amorpha fruticosa, Bouteloua gracilis, Buchloe dactyloides, Dalea purpurea, Helianthus annuus, Solidago rigida, Sisyrinchium angustifolium, Yucca glauca*). E) A comparison of the sticky and artificial grass traps after they were placed in the field. F) artificial grass traps with rabbit droppings. G) Sticky traps covered in ant bodies and leaves.

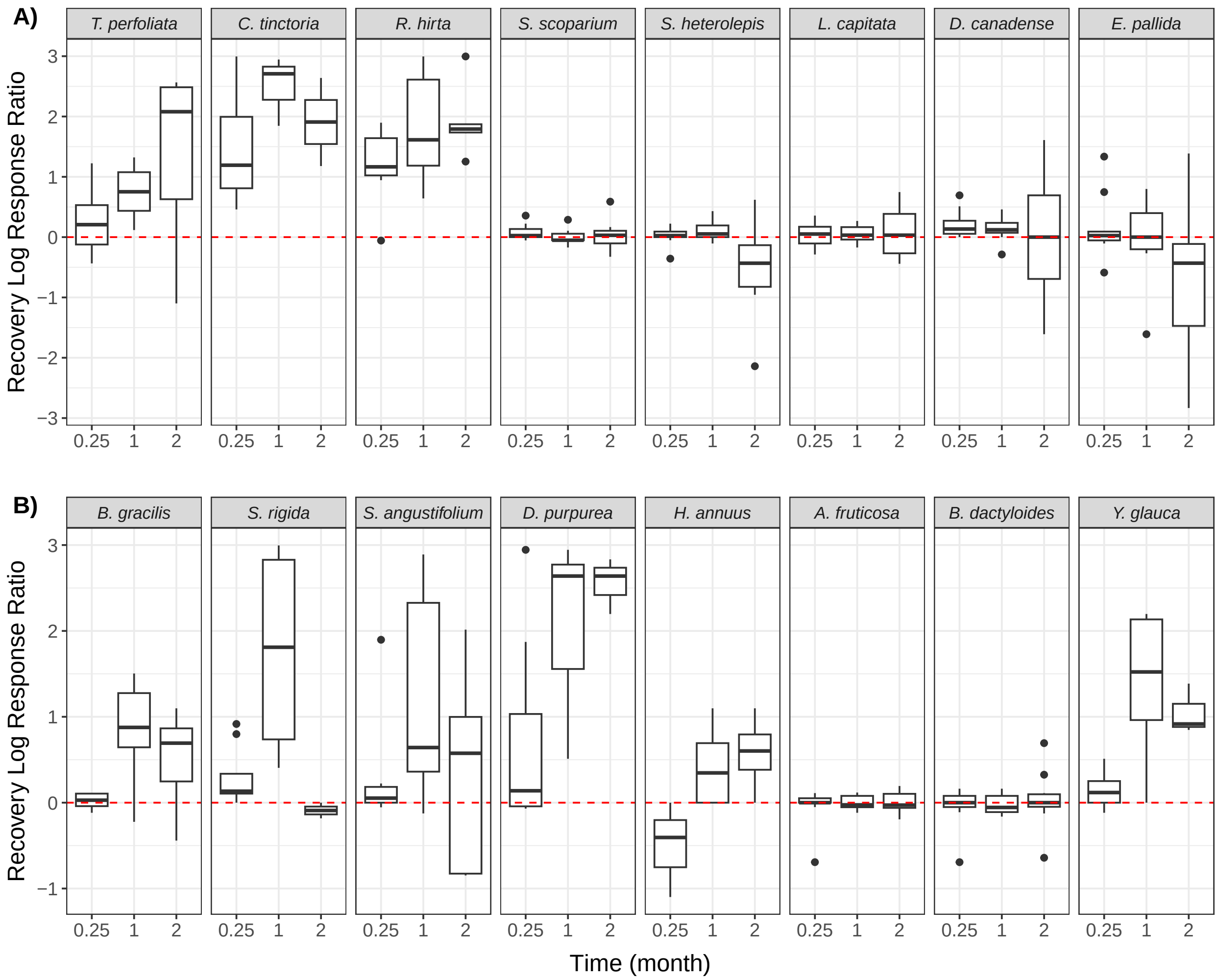

Figure 2: Log response ratio of proportion of seeds recovered in sticky traps relative to proportion of seeds recovered on artificial grass traps from the A) Missouri site, and B) Colorado site. For each state, panels are in seed size ordered from smallest (left) to largest (right). Values of zero (red dashed line) represent equal likelihood of recapture in sticky vs artificial grass traps. Values above zero indicate where seeds were more likely to be recovered on sticky traps. Values below zero represent where seeds more likely to be recovered on artificial grass traps.

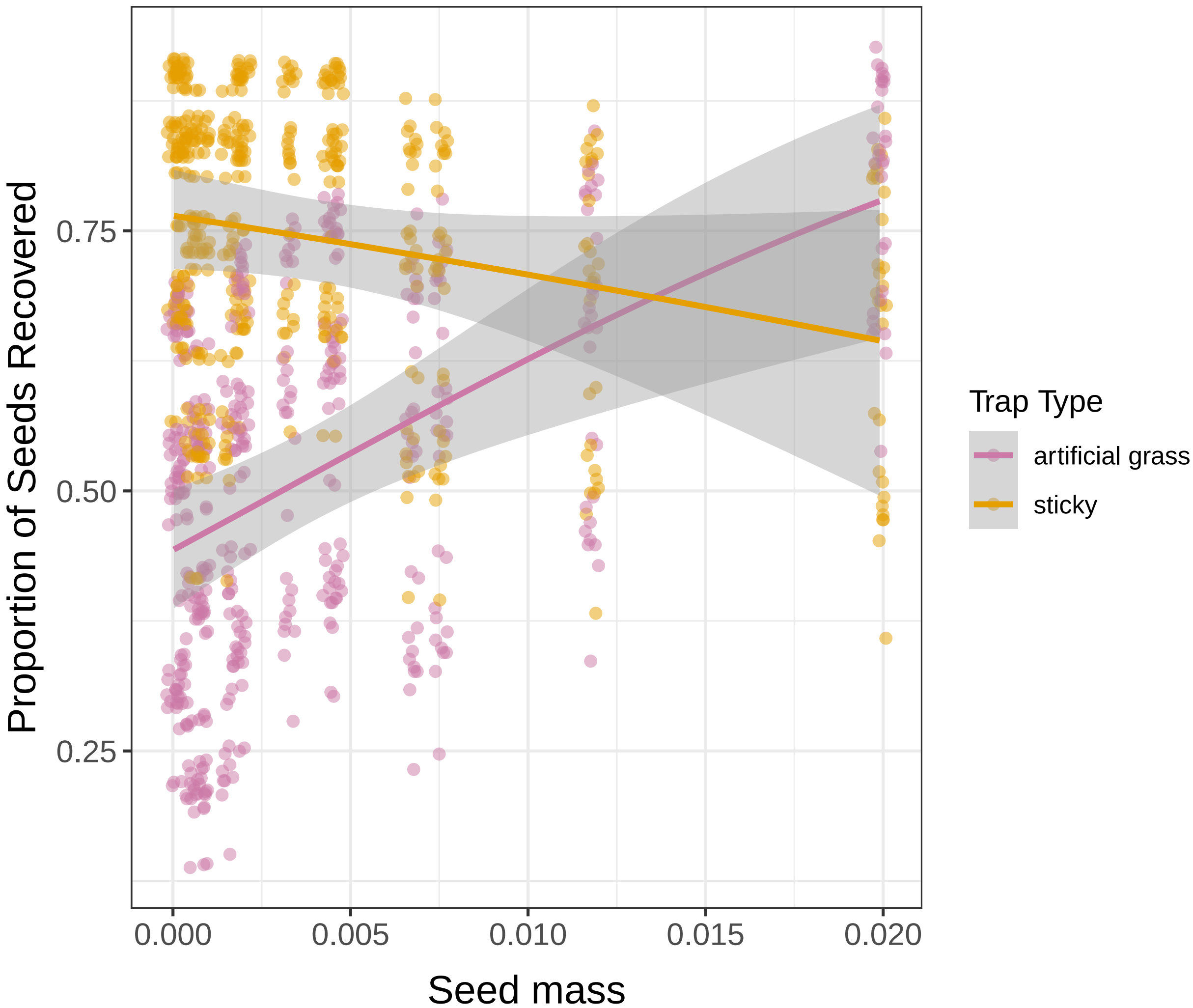

Figure 3: Proportion of seeds recovered in relationship to seed mass with respect to trap type (pink points are artificial grass traps, orange points are sticky traps). As seed mass increases, we find a decrease in the proportion of seeds recovered from sticky traps, and an increase in proportion of seeds recovered from artificial grass traps. Points and lines represent model predicted values.

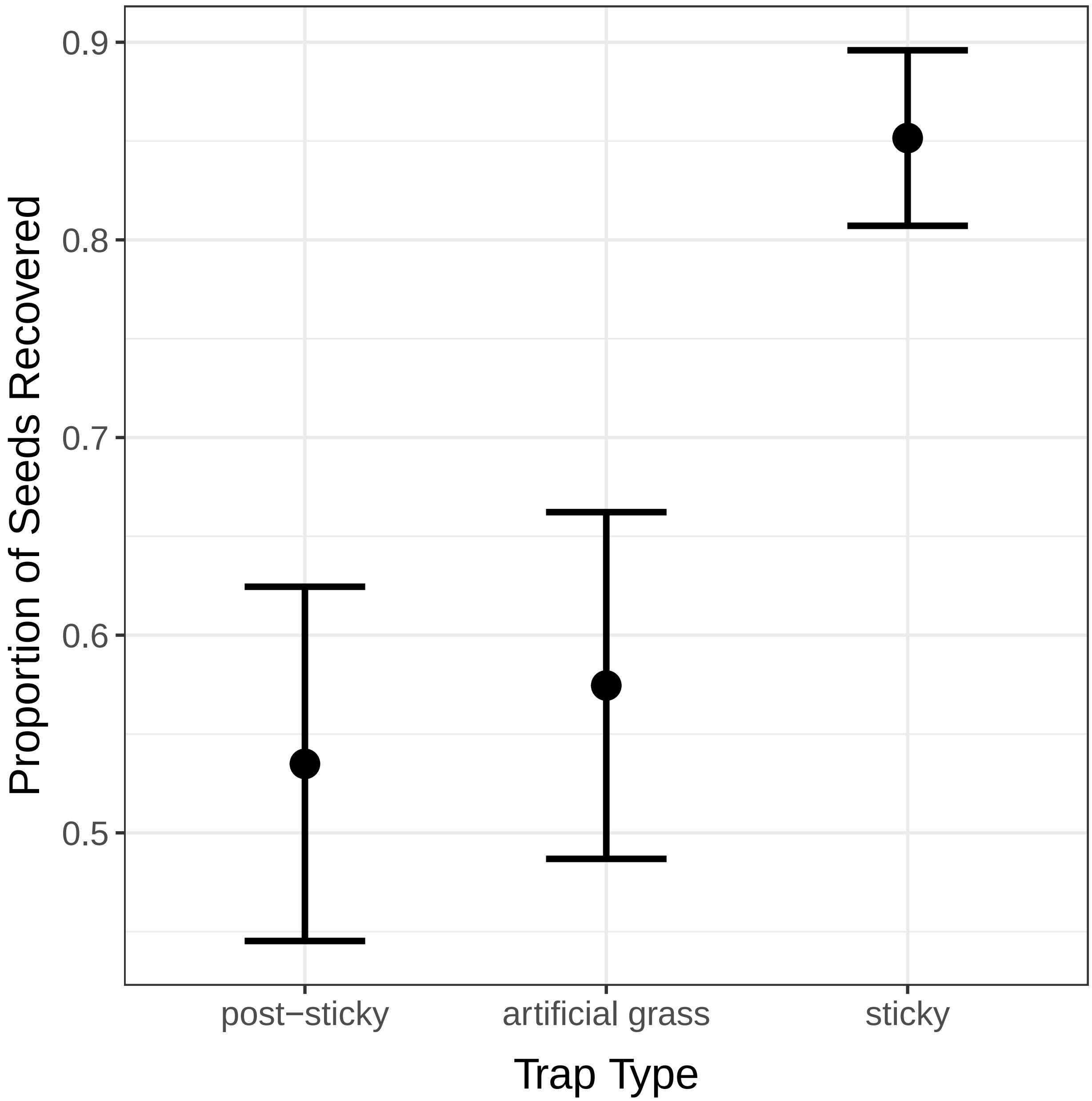

Figure 4: Proportion of seeds recovered with respect to trap type for the traps that had been out in the field for one month in Missouri (i.e. sticky, artificial grass and post-sticky traps). Data are mean model predicted values, and error bars represent standard deviation.