2016 Project Abstract
For the Period Ending June 30, 2020

PROJECT TITLE: Measuring Pollen and Seed Dispersal for Prairie Fragment Connectivity
PROJECT MANAGER: Lauren Sullivan
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FUNDING SOURCE: Environment and Natural Resources Trust Fund
LEGAL CITATION: M.L. 2016, Chp. 186, Sec. 2, Subd. 08b as extended by M.L. 2019, First Special Session, Chp. 4, Art. 2, Sec. 2, Subd. 19

APPROPRIATION AMOUNT: $ 556,000
AMOUNT SPENT: $ 556,000
AMOUNT REMAINING: $ 0

Sound bite of Project Outcomes and Results

This project determined habitat connectivity between prairie fragments by measuring plant movement of 6 species by dispersal of pollen and seeds to improve prairie restoration implementation. New modeling approaches indicated that spillover from established/remanent prairies is a more complicated process than previous thought and requires different land management.

Overall Project Outcome and Results

Outcomes and results are broken down by the papers completed.

Papers Accepted

1. 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.
    - When restored prairies are adjacent to remnant prairies, rare species will move into and establish in these remnant prairies. This is a process we call spillover
    - Species that move into remnants tend to be dispersed by wind or animals.
    - Over 1200 ha of restored prairies benefit from spillover from remnant prairies in Minnesota.
2. Sperry, K. P., Shaw, A. K., & Sullivan, L. L. (2019). Apps can help bridge restoration science and restoration practice. *Restoration Ecology*, 3–6.
    - We created an interactive map for managers in Minnesota to use to determine how landscape connectivity would change when they either 1) removed a remnant prairie, or 2) added a prairie to a location via restoration.
3. Sullivan, L. L., Michalska-Smith, M. J., Sperry, K. P., Moeller, D. A., & Shaw, A. K. (2021). Consequences of ignoring dispersal variation in network models for landscape connectivity. *Conservation Biology*, *35*(3), 944–954.
    - We learned that in Minnesota grasslands, if we model connectivity of our existing habitat fragments by incorporating an actual dispersal kernel, we get very different estimates of connectivity than when we use traditional approaches.
    - This work demonstrates the importance of using dispersal kernels for measuring connectivity.

Papers in Revision

4. Sullivan, L. L., Portlas, Z., Hamilton, J. (In Revision for American Naturalist). Local climate and habitat continuity interact to alter contemporary dispersal potential.
    - *Geum triflorum* dispersal depends on the type of habitat it lives in, as well as the climate in that growing year. As the number of growing degree days increases in prairie habitat, *G. triflorum* disperses farther. However on isolated alvar habitat, as the number of growing degree days increases, *G. triflorum* disperses less distance.

Papers in Prep

5. Radford, Z., Sullivan, L. L., and Moeller, D. (In Prep). Fine-scale maintenance of adaptive genetic variation despite gene flow in a remnant tallgrass prairie.
    - We see evidence of small scale gene flow in *Ratibida columnifera* at Bluestem Prairie, MN.
6. Sullivan, L.L, Radford, Z., Sperry, K., Shaw, A. and Moeller, D. (In prep.) Pollen dispersal of 6 prairie plant species in Northwest Minnesota.
    - We are working to determine the dispersal ability of 6 grassland species.

Project Results Use and Dissemination

This project has been presented at the Ecological Society of America conference in 2018 to an invited session on the role of space for coexistence as well as in 2019. Additionally, our team presented findings at the Botany Society meetings in 2019, 2020, and 2021 and various intuitional research talks in 2019 and 2020. The list of published papers associated with this project can be found in our Overall Project Outcomes.

One of the main outreach foci of this project was to provide conservation agencies and the MPCP with tools that they can use to determine the degree of habitat connectivity and the necessary size of corridors, to promote the spread of desirable species. To that end, we created and an app to the Nature Conservancy, and the MN DNR in March 2019. This app can be found at MN Connectivity.

Date of Report: September 21, 2021

Date of Next Status Update Report: NA

Date of Work Plan Approval: June 7, 2016

Project Completion Date: June 30, 2020

PROJECT TITLE: Measuring Pollen and Seed Dispersal for Prairie Fragment Connectivity

Project Manager: Lauren Sullivan

Organization: University of Minnesota

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Location: Clay County, Minnesota

Total ENRTF Project Budget:		
	ENRTF Appropriation:	**$556,000**
	Amount Spent:	**$556,000**
	Balance:	**$0**

Legal Citation: M.L. 2016, Chp. 186, Sec. 2, Subd. 08b as extended by M.L. 2019, First Special Session, Chp. 4, Art. 2, Sec. 2, Subd. 19

Appropriation Language:

$556,000 the second year is from the trust fund to the Board of Regents of the University of Minnesota to determine habitat connectivity between prairie fragments by measuring plant movement by dispersal of pollen and seeds to improve prairie restoration implementation. This appropriation is available until June 30, 2019, by which time the project must be completed and final products delivered.

Carryforward; Extension (a) The availability of the appropriations for the following projects is extended to June 30, 2020: (12) Laws 2016, chapter 186, section 2, subdivision 8, paragraph (b), Measuring Pollen and Seed Dispersal for Prairie Fragment Connectivity;

I. PROJECT TITLE: Measuring Pollen and Seed Dispersal for Prairie Fragment Connectivity

II. PROJECT STATEMENT:
WHY: Connections among habitat fragments are changing across Minnesota. These changes help some plant species while impairing others. Unfortunately, it is not always desirable species that benefit and undesirable species that are harmed. The **GOALS** of this project are to measure prairie plant connectivity to 1) promote the movement of desirable (e.g.: native) species by natural processes, or proper corridor creation, by 2) providing essential information about movement to the Minnesota Prairie Conservation Plan (MPCP).

This project will achieve the following **OUTCOMES:**

1. Measure the pollen and seed dispersal distances for 8 representative native Minnesota prairie species.
2. Determine connectivity of prairie fragments, which informs:
    a. Restoration practices for Minnesota conservation agencies.
    b. Decisions about the appropriate distances for sources of local-ecotype seed.
3. Provide conservation agencies and the MPCP with tools that they can use to determine the degree of habitat connectivity and the necessary size of corridors, to promote the spread of desirable species.

HOW: By measuring plant pollen and seed movement among habitat fragments, we can quantify habitat connectivity. This project will increase the success of the MPCP and other Minnesota restoration projects by understanding how well habitat corridors, and prairie fragments function to move species.

Background: Since 1908, Minnesota has lost 99% of its 18 million acres of remnant prairie. In addition to the overall loss in area, the prairie habitat has also become fragmented into increasingly smaller pieces. Prairie habitat can only persist as long as prairie plant and animal species are able to move among fragments, ensuring their connectivity. Having sufficient connectivity is important for maintaining important ecological and human services including habitat for pollinators and other wildlife, soil stability, water quality, and high quality land for hunting and other recreational activities. It is necessary to know how far plant species move by pollen or seeds, in order to critically evaluate how well Minnesota conservation projects connect prairie habitats.

Minnesota is currently investing large amounts of money and effort into prairie restorations and corridor creation, through the MPCP. However, this project was created by making assumptions of how far plants and animals move down corridors and between fragments. Since it is unknown how far plants move between restored areas, it is difficult to determine how successful these restoration projects will be. Our project will supply the MPCP and other conservation agencies with crucial movement information that can be immediately implemented by the MPCP to improve the quality of prairie corridors and other restorations across the state.

Premises and Hypothesis

I. **Maintaining plant connectivity between prairie fragments depends on how far species can disperse, and is essential for increasing both species and genetic diversity in fragments. Connectivity can in turn have a positive effect on other members of the prairie ecosystem, including pollinators and other wildlife.**

II. **Determining how far plants disperse has been difficult in the past due to the difficulty tracking tiny pollen grains and seeds. However, with advances in sequencing techniques, it is now possible to use genetics to determine how far species are moving on a large subset of species. Dispersal distances must be measured in order to understand prairie fragment connectivity.**

III. **Plants have different dispersal syndromes, or ways their pollen and seeds disperse (e.g.: pollen and seeds disperse by wind, pollen disperses by animals and seeds disperse by wind, pollen disperses by**

wind and seeds disperse by animals, and both pollen and seed disperse by animals). We believe these syndromes will differ in how far their pollen and seeds disperse. The literature does not provide a comprehensive test of how these syndromes differ in their pollen and seed dispersal distances, and this must be measured.

IV. Landscape connectivity will depend on the dispersal ability of plant species. Animal pollinated species will disperse farther and therefore be more connected than wind pollinated species. Animal dispersed seeds are more connected than wind dispersed seeds. Finally, within the wind-dispersed seeds, traits such as height, terminal velocity, morphology are important drivers of connectivity.

III. OVERALL PROJECT STATUS UPDATES:

Project Status as of *July 22, 2016:*

Amendment Request (07/22/2016):

I would like to purchase a GPS system because all rental options were not accurate enough. The GPS system I would like to purchase costs $4500, and includes the Trimble R2 sub-foot Rover GPS unit (which can provide up to centimeter accuracy in open grasslands), the Terraflex software necessary for collecting and processing data, and the mounting equipment for the GPS unit. I propose to move $4500 from the travel budget (per diem is no longer needed this year) to the equipment/tools/supplies budget.

Amendment Approved (07/22/2016)

Project Status as of *January 1, 2017:*

We began work on this grant by establishing our field sites and collecting field data on three of our target species (Activity 1), as well as collecting connectivity data at many adjacent prairie sites (Activity 2). We are currently working to extract DNA from these species and germinate the offspring necessary to estimate pollen dispersal distance (Activity 1). Over the last reporting period we have worked with three recently graduated biology technicians, and collaborated with many people, including: 4 faculty from MSUM, 1 faculty from NDSU, 1 person from the SNA program, 2 people from TNC, and 1 person from FWS. We have presented at one local scientific meeting (for the Nature Conservancy – approx. 35 people in attendance), and volunteered to lead two outreach activities: one for Scientific and Natural Areas (SNA) stewards in the Clay County area (through the SNA program – 6 people) and one for the MSUM undergraduate summer interns (through MSUM – 15 students).

Amendment Request (12/20/2016):

I am requesting that some of our travel funds be allocated for costs associated with attending the National Native Seed Conference in Washington DC in February 2017 and presenting on this work. This conference is a great opportunity to get new ideas about how to perform this project better, and also to inform scientists, land managers and policy makers from around the country about the work that we are doing in Minnesota to understand prairie connectivity and movement. The costs associated with the conference include $400 registration, $350 flight, $900 hotel ($1650 total) – I propose to re-allocate some travel funds for the conference.

Amendment Approved (12/28/2016)

Project Status as of *July 1, 2017:*

Over the last reporting period, we extracted DNA from both the parental generation and offspring generation of one of our target species. We have also decided to use the sequencing facility at the University of Minnesota to sequence our samples. We are currently running pilot studies for our three collected target species to determine how easily we can sequence our samples, and for what cost. The 2017 field season has also begun and we have begun collecting data from three new target species, for a total of 6 out of the proposed 8 target prairie species. We have hired two new field techs, one recently graduated biology student, and anther who will begin her senior year this coming fall. We have also presented our work at one national conference (the National Native Seed Conference – 330 people in attendance, including scientists, land managers and the native seed industry), and one for the MSUM undergraduate summer interns (through MSUM – 7 students).

Project Status as of *January 1, 2018:*

We accomplished a lot on this project over the last reporting period. We finished tissue and data collection for our full set of 8 species as promised under our work plan. We have now collected tissue from over 2000 individuals of our 8 target species and collected seeds to germinate from all 8 species. Over the summer we trained two highly accomplished field technicians who have now moved on to full-year science technician positions. In collaboration with these two technicians, we developed a scientific study to look at which species are moving on the landscape, and if remnant prairies can act as sources of rare species for reconstructed prairies. We found that when low-diversity reconstructed prairies are adjacent to remnant prairies, there is evidence of rare species spilling over into these reconstructions up to 50m (Supplemental Figure 2). We are currently working on publishing our findings. Additionally, we are still working with the University of Minnesota genetics group to help us sequence the DNA of our species. There has been a lot of trial and error due to the difficulty of working with non-model plant species. However, we continue to work closely with them, and should have results from our first species in a month or two; after which we can begin building our dispersal kernels.

Amendment Request (02/06/2018):

First, we did not end up purchasing our own GPS unit because we found one we could rent from the University for much less money. So I would like to move $800 of the money for purchasing the “subfoot accuracy GPS unit” to a new category within “Equipment/Tools/Supplies” called GPS rental. Then, I request that we move the rest of the $3700 for the GPS purchase to the “Equipment/Tools/Supplies” – Field and Lab Supplies to cover the cost of extra supplies we will need for extracting DNA and for sampling plants in the field. Finally, due to unexpected slowness in the sequencing facility, I need to change a few of my completion date deadlines within Activity 1 and Activity 2 (see below).

Amendment Approved (02/15/2018)

Project Status as of *July 1, 2018:*

During the past reporting period we have focused on continuing to grow seedlings and extract DNA from plant tissue. We have now extracted DNA from all individuals of 3 of the 8 target species, and are partially finished with 2 more. Due to the strict nature of requirements by the sequencing facility, and the time it takes to extract DNA to that standard, we are asking for an amendment to move some of our money to pay for the facility to also extract DNA for us for a few of the species that remain (see amendment request below). After a lot of back and forth and needing to re-do sequencing, we have a full set of sequence data for one of our target species from the sequencing facility and we plan to begin creating dispersal kernels within the next month.

Amendment Request (07/03/2018):

We need to move a few budget items around to make sure we have enough money for supplies and field travel, and to adjust for a few budget items that cost less than anticipated. Sequencing is costing ~$5000 less than anticipated, and we did not need to rent the GPS again, so we have another $246 surplus. I would like to add ~$3000 for field and lab supplies, ~$2700 for travel to field sites. In doing this, we have moved money for supplies from activity 2 to activity 1 to make budgeting simpler and because activity 1 requires more supplies. Finally, we need to update the timeline for creating the dispersal kernels for our 8 target species. Working to get the DNA sequenced has proven to be a difficult task as our sequencing facility (UMGC) is doing a lot of troubleshooting with our data and thus running into road blocks. This means it is just taking longer to get the work completed. We are doing our best to get remainder of our samples sequenced as soon as possible.

Amendment Approved (Amendment Approved by LCCMR 8/28/2018)

Project Status as of *January 1, 2019:*

In the last reporting period, for Activity 1 we finished sequencing the DNA from two species, and a third should be finished in the next month or two. We have also run pilot projects on the final four species with the sequencing facility to make it easier to sequence the DNA from all individuals once the offspring have finished germinating and have enough tissue to extract from (which should be done within the next month). For Activity 2 we have completed general connectivity models and have written up a manuscript that will be submitted for publication within the upcoming reporting period. These models can be modified to fit our dispersal kernels that we create once we have all of our sequencing completed. For Activity 3 we have made a lot of progress within the last reporting period. We have developed a web-based application for managers where they can select the county they are in within Minnesota, and determine which prairies in the county are connected based on various dispersal distances. We are planning multiple events where we demonstrate this application to land managers, in order to present it to them for Activity 3. Finally, our side project that was developed by the technicians on the project to look at native species spillover from remnant prairies to restored prairies is under review in the Journal of Applied Ecology. See Supplemental Figure 3 for a one-page summary of our research findings that can be shared freely.

Amendment Request (12/28/2018):

We are requesting a Legislative Extension for our project to move the end date to October 31, 2019. Due to issues outside our control, we have been unable to complete the sequencing for Activity 1 as quickly as we originally planned. In short, the sequencing facility we originally planned to use shut down operation and so we had to develop a completely new system with the University of Minnesota Genomics Center (UMGC). It has taken quite a while to trouble shoot our methods with our non-model native prairie plant species and so we are not yet finished with all of the sequencing for Activity 1. Should we not receive the extension, the results we can provide on plant species connectivity from our project are very general. If we receive a Legislative Extension, we will be able to provide much more targeted connectivity information about specific rare species in the state of Minnesota. This information will be passed on to land managers throughout the state (we already have made these connections), and will be able to provide information to the Minnesota Prairie Conservation Plan as to the dispersal and connectivity abilities of plant species, which is currently missing.

Amendment Request signed into law 5/31/19

Project Status as of *July 1, 2019:*

We have made incredible progress in the last reporting period. First, we cleaned up all tags from plants at Bluestem Prairie for Activity 1. Additionally, we are extremely close on finishing all of the sequencing for our target species, and have just two more species to sequence. Which means we have finished the sequencing for 5 of our total 7 target species. Additionally, we have submitted our first research paper from Activity 2 for publication and we just received positive reviews at Conservation Biology. Once this project is accepted for publication we will create a 1 page summary that can be shared freely. Our side project on species spillover is now accepted for publication at the Journal of Applied Ecology and can be found at this website (https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2664.13469) Finally we have made fantastic progress on Activity 3. We developed the web-based application for how managers in Minnesota can implement connectivity analyses on the grasslands in their county (https://grassland-connectivity.shinyapps.io/MNConnectivity/). We held several meetings to beta-test the app, including a meeting with the MN, ND, SD TNC chapter. A web-based tutorial is now available here (https://www.youtube.com/watch?v=bS93mnMyAW8), and we will be presenting this app to other Minnesota land managers in the fall. We also published a paper on the usefulness of apps for conservation management in Restoration Ecology and can be found here (https://onlinelibrary.wiley.com/doi/10.1111/rec.12999).

Amendment Request (08/02/2019):

I am requesting a few changes to the budget to help us use up the rest of the money. It turns out we need a bit more money for hiring people to help us process our samples and analyze our data, and we need a bit more money for lab supplies to make this happen. Fortunately, we do not need quite as much money as we anticipated for sequencing, and the rest of our Activity 3 work is completely virtual so it requires no money to conduct.
Amendment Approved (08/20/2019)

Project Status as of *January 1, 2020:*
Over the last 6 months we have been working on analyzing our genetic data to perform paternity analysis and extract dispersal kernel information from the data. We are making progress and are starting to feel comfortable with the pipelines to do the work, however we keep finding issues with the genetic data that we need to deal with. I believe this will be worked out soon. All sequencing for the project has been completed!

Project Status as of *July 1, 2020:*
We have completed the sequence analysis of our genetic data and have finished our models as well. We have published 3 scientific papers from this work (from the modelling, the fieldwork and the interactive app), and are working on two more papers on the genetic data.

Overall Project Outcomes and Results:

Outcomes and results are broken down by the papers completed.

Papers Accepted

1. 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.
    - When restored prairies are adjacent to remnant prairies, rare species will move into and establish in these remnant prairies. This is a process we call spillover
    - Species that move into remnants tend to be dispersed by wind or animals.
    - Over 1200 ha of restored prairies benefit from spillover from remnant prairies in Minnesota.
    - We presented on this work at the Ecological Society of America conference in 2018 to an invited session on the role of space for coexistence.
2. Sperry, K. P., Shaw, A. K., & Sullivan, L. L. (2019). Apps can help bridge restoration science and restoration practice. *Restoration Ecology*, 3–6.
    - We created an interactive map for managers in Minnesota to use to determine how landscape connectivity would change when they either 1) removed a remnant prairie, or 2) added a prairie to a location via restoration.
    - You can find this interactive app here: https://grassland-connectivity.shinyapps.io/MNConnectivity/
    - We presented on this app to the Nature Conservancy, and the MN DNR in March 2019
3. Sullivan, L. L., Michalska-Smith, M. J., Sperry, K. P., Moeller, D. A., & Shaw, A. K. (2021). Consequences of ignoring dispersal variation in network models for landscape connectivity. *Conservation Biology*, *35*(3), 944–954.
    - We learned that in Minnesota grasslands, if we model connectivity of our existing habitat fragments by incorporating an actual dispersal kernel, we get very different estimates of connectivity than when we use traditional approaches.
    - This work demonstrates the importance of using dispersal kernels for measuring connectivity.
    - We presented on this work at the Ecological Society of America conference in 2019.

Papers in Revision

4. Sullivan, L. L., Portlas, Z., Hamilton, J. (In Revision for American Naturalist). Local climate and habitat continuity interact to alter contemporary dispersal potential.
    - *Geum triflorum* dispersal depends on the type of habitat it lives in, as well as the climate in that growing year. As the number of growing degree days increases in prairie habitat, *G. triflorum* disperses farther. However on isolated alvar habitat, as the number of growing degree days increases, *G. triflorum* disperses less distance.
    - We presented on this work at the Botany Society meeting in 2019, and at various institutional research talks in 2019 and 2020.

Papers in Prep

5. Radford, Z., Sullivan, L. L., and Moeller, D. (In Prep). Fine-scale maintenance of adaptive genetic variation despite gene flow in a remnant tallgrass prairie.
    - We see evidence of small scale gene flow in *Ratibida columnifera* at Bluestem Prairie, MN.
    - We presented on this work at the Botany Society meeting in 2021.
6. Sullivan, L.L, Radford, Z., Sperry, K., Shaw, A. and Moeller, D. (In prep.) Pollen dispersal of 6 prairie plant species in Northwest Minnesota.
    - We are working to determine the dispersal ability of 6 grassland species.

IV. PROJECT ACTIVITIES AND OUTCOMES:

ACTIVITY 1: Measure pollen and seed dispersal distances for native prairie species

Description: We propose to determine how far plants are moving by pollen and seed using a combination of DNA paternity analysis and GPS location data (See attached Figure). In this way, we can know how far related individuals are from each other. By aggregating all measured movement distances from each species, we can create both pollen and seed dispersal kernels for all of our target species. These kernels can be compared across dispersal syndromes to determine which types of species will move farther than others. For example, we can determine if species with animal pollination and animal-dispersed seeds move farther than animal pollination and wind-dispersed seeds.

Our work for Activity 1 takes place in Clay County, Minnesota. We chose this location as it contains large swaths of remnant prairie that have never been plowed. When determining the dispersal kernel of these species, we must be able to match parents and offspring. Thus, it is important to work in a prairie without human-caused seed additions because during a restoration many seeds from unknown parental sources are seeded randomly at one time, making movement and paternity determination difficult. We are proposing to work within Bluestem Prairie, a remnant tallgrass prairie on the Lake Agassiz Beach Ridge (See attached Figure with map). We visited the site in early November 2015 to determine the likelihood of project success at the site, and determined it would be an ideal site.

The primary goal of Activity 1 is to create dispersal kernels for our 8 target species (Table 1) within a large, continuous remnant prairie in order to maximize our ability to detect long distance dispersal. In the first year (summer 2016) we will focus on four of our eight target species in order to refine our methodology, and finish collecting data from our remaining target species in the second year (summer 2017). Then, time and money permitting, we will sample near-by smaller remnant habitat fragments in order to detect connectivity between distant habitat patches, and to see if species' dispersal kernels are similar between large, continuous prairies and smaller, more fragmented prairies.

Species	Latin name	Dispersal syndrome
Prairie dropseed	*Sporobolus heterolepis*	**syndrome I** pollen: wind; seed: wind
Big bluestem	*Andropogon gerardii*	**syndrome I** pollen: wind; seed: wind
Blazing star	*Liatris aspera*	**syndrome III** pollen: animal; seed: wind
Sawtooth sunflower	*Helianthus grosseserratus*	**syndrome III** pollen: animal; seed: wind
Showy milkweed	*Asclepias speciosa*	**syndrome III** pollen: animal; seed: wind
Coneflower	*Echinacea angustifolia*	**syndrome III** pollen: animal; seed: wind
American licorice	*Glycyrrhiza lepidota*	**syndrome IV** pollen: animal; seed: animal
Prairie rose	*Rosa arkansana*	**syndrome IV** pollen: animal: seed: animal

Table 1: List of proposed target species we will focus on for this project and their dispersal syndromes.

In order to create our proposed dispersal kernels, we will be collecting leaf and pollen tissue and GPS location data from all individuals of our 8 target species within our sampling area at Bluestem Prairie. We will then run genetic paternity analysis on all of our samples to determine which individuals are most closely related to which other individuals. We then calculate the distance between each parent and offspring in a pair, to determine the distance that the offspring's seed must have traveled (seed dispersal distance), and combine all the seed dispersal distances for all individuals within each target species and calculate the probability of dispersing all possible dispersal distances for this species. This is the seed dispersal kernel. We use a similar method to calculate the pollen dispersal kernel. We match pollen that has landed on a mother plant to a father plant (the pollen's origin) using DNA parentage analysis. We calculate the distance between the father plant and the mother plant, to determine the distance that the father's pollen must have traveled (pollen dispersal distance). Again, we combine all the pollen dispersal distances for all individuals within each target species and calculate the probability of dispersing all possible dispersal distances, or the pollen dispersal kernel.

Summary Budget Information for Activity 1:		
	ENRTF Budget:	**$ 417,575**
	Amount Spent:	**$ 417,575**
	Balance:	**$ 0**

Outcome	Completion Date
select sites and receive permits to sample	*July 2016*
collect tissue samples for first 4 target species	*November 2016*
extract DNA from first 4 target species	*June 2017*
send samples out for sequencing and receive genetic data	*November 2017*
run paternity analysis on first set of target species	*June 2018*
create dispersal kernels for first set of target species	*February 2019*
collect tissue samples for remaining 4 target species	*November 2017*
extract DNA from remaining 4 target species	*December 2018*
send samples out for sequencing and receive genetic data	*August 2019*
run paternity analysis on remaining set of target species	*September 2019*
create dispersal kernels for remaining set of target species	*September 2019*

Activity Status as of *January 1, 2017:*

We successfully selected sites for Activity 1 work in Clay County and received the appropriate permit for our study. We are working at Bluestem Prairie, which is primarily managed by The Nature Conservancy. From July to the end of September, we worked to collect tissue samples from 3 of our target species including *Ratibida* *columnifera*, *Echinacea angustifolia*, and *Solidago rigida*. These three species are slightly different from our proposed species in Table 1, and will replace a few species in Dispersal Syndrome III: pollen dispersed by animals and seeds dispersed by wind. These species were chosen because they were the species that were in the appropriate densities at the site to sample (i.e., not too many, not too few). We had hoped to collect from 4 target species this year, but due to the late start in the season many species were past flowering/seed set. We could not start collecting until around August 1 because it took some time to get the sites selected and our equipment ordered after July 1. We did manage to successfully survey 3.5 hectares of Bluestem prairie for: 408 individuals of *R. columnifera*, 591 individuals of *S. rigida*, and 322 individuals of *E. angustifolia*. We collected location data and tissue samples from all of these individuals, which represent ~95% of all flowering individuals in the study area - we likely missed a few, but this varied by species. We are currently beginning the work of extracting the DNA from our collected target species. This include growing up offspring from select moms to collect tissue from and sequences in order to determine pollen dispersal distance. We should be on track to finish these three species by June of 2017 as we proposed above.

Activity Status as of *July 1, 2017:*

We are continuing to stay on track for Activity 1. We have successfully extracted DNA from all parents of one species (*R. columnifera*), and grown up over 450 offspring from each of two of the target species (*R. columnifera* and *S. rigida*). While we promised to have all of the DNA extracted from our first three target species by June 2017, we have not quite finished this yet. We decided to take a more conservative approach, where we submit DNA samples from our three target species to be sequenced by the facility at the University of Minnesota to determine how likely our project is to work before we spend too much time and money extracting the DNA from all of our samples from our currently collected 3 target species. This pilot study is under way, and once it is complete and we get the go-ahead, we will be able to extract and sequence all of our target species quickly. While we are waiting for the results we have perfected the DNA extraction technique for each species, so as to be prepared when we get the "ok".

Over the winter, we created a map of our sampled target species, so we could see spatial patterns of where our individual target species were found within the sampled 3.5 ha (Supplemental Figure 1). This spring, we begun a second field season, and have collected tissue from 3 more target species at our site, including *Geum triflorum* (in order to partner our work with that of Dr. Jill Hamilton at North Dakota State University), *Penstemon grandifloras*, and *Oxytropus lambertii*. These species vary in flowering phenology and dispersal mode in order to sample a wide range of rare prairie plant species. The field sampling process is going smoothly this year, and we expect to finish our 8 target species on schedule this season.

Activity Status as of *January 1, 2018:*

The field work portion of this project is on track for Activity 1. As proposed, we have collected tissue from all 8 of our proposed target species. It was difficult to find species that fit nicely into the dispersal syndrome categories (Table 1) that were in the appropriate abundances in the field, and were also diploid (which makes the paternity analysis possible). Thus, we focused our efforts on collecting from a range of insect pollinated, wind or animal dispersed species (syndrome III and IV), although we were able to collect from one wind pollinated, wind dispersed species (syndrome I). This new subset of species will give us a richer idea about how pollen is moving in prairies, and how plant species are serving as resources for pollinators.

In working with my two summer technicians, Jessica Peterson from the MN DNR, and Ian Lane from University of Minnesota, we developed an observational study to determine if we are seeing species move on the landscape. If we see evidence for this, it would give credence to the importance of understanding how species move more fully (the rest of the project). The movement of target species from one habitat to another is often called spillover. We examined if spillover was occurring from high quality remnants into adjacent reconstructed prairies (seeded with both high and low diversity). We found that spillover of rare prairie species does in fact occur from remnant prairie sources, but we only see evidence of it in low diversity reconstructed prairies. The spillover effects occurred up to 50m away from the remnant prairie (Supplemental Figure 2). We are currently working to publish this information in a peer reviewed journal.

The last piece of Activity 1 is the genetic sequencing component. We are a bit behind schedule here, but this is unfortunately unavoidable. There has been a lot of difficulty in developing the methods for extracting and sequencing the DNA from these non-model plant species. However our team has been doing a fantastic job of facing these challenges and continuing to move forward despite many delays. We have extracted DNA from two full sets of target species (~300 *Ratibida columnifera* and 500 *Solidago rigida* individuals). In addition, we have grown up offspring for these two species (~450 offspring for each species). Our lab technician is also beginning to explore the population-level trait variation in these offspring. We had a lot of difficulty germinating offspring from *Echinacea angustifolia*, one of our target species collected in 2016. However we recently began to see germination so we hopefully have that protocol down now. We should be hearing back from the sequencing facility in the next month or two on our first complete species (*R. columnifera*), and should be able to begin data analysis soon. The first attempt to sequence this species was not fully successful, so much of the work had to be repeated. The sequencing facility seems confident everything should work out this time around.

Activity Status as of *July 1, 2018:*

We are generally still on track to meet our deadlines for Activity 1 above. We have received our first set of full sequences from the sequencing facility for one species (*Ratibida columnifera)*, and so can begin to create pollen dispersal kernels. We have submitted a full set of extracted DNA from our second species, *Solidago rigida* and they are going through the sequencing process currently. This will hopefully be faster than for *R. columnifera* because of the base work we have put in already. We had difficulty extracting DNA from our third species, *Echinacea angustifolia,* but we are getting close here, and should have that submitted soon. We are now beginning to extract DNA from our fourth and fifth species, *Penstemon grandiflourus* and *Geum triflorum*.

We are also making good progress on the observational study in collaboration with Ian Lane (University of Minnesota grad student) and Jessica Peterson (Scientist at MN DNR). The manuscript is complete and has gone through several rounds of peer-editing. We are planning to submit the paper for publication in August, 2018.

Activity Status as of *January 1, 2019:*

We have completed the sequencing process for two species (*Ratibida columnifera* and *Solidago rigida*) and should be finished with the sequencing of the third species (*Echinacea angustifolia*) within the next few months. We are in the process of running the paternity analysis and creating the dispersal kernels for these first two species, and it will be relatively straightforward to complete this process for the rest of the species once we have completed the process once. The final four target species (*Penstemon grandiflorus, Geum triflorum, Delphinium carolinianum,* and *Artemisia frigida*) have had their pilot testing run with the sequencing facility and thus are ready to be sequenced fully when the offspring tissue is grown. This should be finished within the next month, and we will submit the tissue samples for these last four species at that time. Finally, we have decided to drop our eighth species (*Oxytropus lambertii*) because we could not get a complete enough sample of its population in the field, and we worry we would not get good sequencing results. Thus we feel we have acted in the spirit of the grant by trying as hard and collected tissue from 8 target species, but only the collections for 7 of these are adequate for sequencing.

Our observational study with Ian Lane and Jessica Peterson is now under review at the Journal of Ecology. Supplemental Figure 3 provides a 1 page summary of the project and our results and can be shared freely.

Activity Status as of *July 1, 2019:*

We have completed the sequencing for 5 of our 7 target species, including *Ratibida columnifera*, *Echinacea angustifolia*, *Solidago rigida*, *Artemisia frigida*, and *Geum triflorum*. Our last two target species, *Penstemon* grandiflorus and *Delphinium carolinianum* are both halfway through the process of DNA extraction and sequencing and should be completed soon. We have cleaned up all tags and flags from Bluestem Prairie in order to eliminate eco-waste, and thus we are completely done in the field. We are currently in the process of calculating dispersal kernels for our species.

Activity Status as of *January 1, 2020:*

We have completed sequencing for 6 of our 7 target species: *Ratibida columnifera*, *Echinacea angustifolia*, *Solidago rigida*, *Artemisia frigida*, *Geum triflorum*, and *Penstemon grandiflorus*. We unfortunately ran out of funds halfway through sequencing *Delphinium carolinianum*, and thus will not be able to finish this species unless we can find another ~$12,000. So we will move on without this species and see if we can round up the funds. We are working through how to determine paternity using computer-based pipelines but it is a process that takes a lot of tweaking. We believe that we are getting close, and as soon as we are able to feel confident in our paternity assignments, then we will be able to calculate our dispersal abilities and dispersal kernels.

Final Report Summary:

We have finished the paternity analysis for our 6 species, and are working to determine the dispersal ability for all of these species. See Table 1 for the species we have finished.

Table 1: Mean and Max pollen dispersal distances for the species we have finished analyzing/

Species	Mean Pollen Dispersal Distance	Max Pollen Dispersal Distance
Ratibida columnifera	118m	351m
Artemisia frigida	23m	228m
Penstemon grandifloras	112m	368m

ACTIVITY 2: Determine connectivity of prairie fragments in NW Minnesota

Description: Once we know the dispersal kernels of our target species, we can determine the connectivity of the prairie fragments in Clay County for those species using connectivity network analysis. This connectivity work will span across remnant and restored prairies. We can then test our hypotheses that connectivity networks vary by dispersal syndrome and dispersal traits. We also have the ability to make estimates of dispersal kernels of non-target species that are similar to the targets, and determine connectivity of those species as well, to better characterize the community.

We will use the dispersal kernels measured in Activity 1 to parameterize network models that can inform Clay County of the connectivity of its grasslands. Within a defined region of Clay County, we will sample all of the grassland fragments for species richness. We will likely choose the area surrounding Bluestem Prairie where we are measuring the dispersal kernels, but the decision will ultimately depend on where we can utilize previously conducted fragment richness surveys. If previous sampling methods match our methods, we will use existing data instead of collecting the data ourselves.

During the 2016 and 2017 summer field seasons, we will survey the plant species richness of the prairie fragments in Clay County. We will also use GIS to spatially locate each of the prairie fragments. Then, combining these two datasets, we will create connectivity networks where we estimate how connected the prairie fragments are based on the species richness, the pollen and seed dispersal distance of each target species, and the distance of each fragment to each other. This information is useful for planning precision prairie restorations as we can determine locations where new restorations would greatly increase connectivity on the landscape.

We may also be able to generalize our connectivity results to a broader range of prairie plant species than just the 8 target species that we measure. If, in Activity 1, we find that species with different dispersal syndromes consistently have different dispersal kernels, we can infer that non-target prairie species with the same dispersal syndromes are likely to have similar dispersal kernels as the species we measured. Thus, we will potentially be able to infer connectivity for any prairie plant species, as long as we know how its seeds and pollen are dispersed.

Summary Budget Information for Activity 2:		
	ENRTF Budget:	**$ 138,412**
	Amount Spent:	**$ 138,412**
	Balance:	**$ 0**

Outcome	**Completion Date**
determine which prairie fragments to survey in Clay Co.	*August 2016*
get permission to survey selected prairies	*September 2016*
begin richness surveys in downtime from sampling tissue	*November 2016*
complete richness surveys in downtime from sampling tissue	*November 2017*
Create general connectivity models	*December 2018*
determine connectivity for all target species	*October 2019*

Activity Status as of *January 1, 2017:*

We are on schedule for Activity 2 within the last reporting period. We were able to determine which sites we wanted to sample and received permission in June 2016. We sampled many of the remnant and restored prairies that were adjacent to Bluestem prairie this field season for richness and abundance. We sampled 7 restored prairie sites, and 7 remnant prairie sites with 15 vegetation plots at each site. We will continue this work in prairies that are more distant from our main study site at Bluestem Prairie in the upcoming year. We have those sites selected and know how to obtain the collecting permits before the upcoming field season. We are currently in the process of cleaning up the data and beginning to get the models together that can look at connectivity between prairies. While we will not know the exact dispersal distances of our target species for a while, we will be able to get our models set up so it is simple to plug that information in once we have it (proposed approx. February 2018).

Activity Status as of *July 1, 2017:*

We have begun analysis to compare the plant communities between restored and remnant prairies sampled last year. We are in the process of beginning to create connectivity models of our prairie sites, and will also continue to sample the plant community at many sites throughout the region. The plants have just greened up enough for us to begin community sampling, which we will do over the next few months in our down time from sampling the individual target species.

Activity Status as of *January 1, 2018:*

We continue to be on target for this project. We are likely to need to sample more communities next summer. This will be determined by the connectivity models we create over the next reporting period.

Activity Status as of *July 1, 2018:*

Again, we continue to be on target for this Activity, although we need to extend the exact deadline for the species connectivity out because of the speed of sequencing. We are currently working on the general models that will help predict landscape-level connectivity of all the species. This way, when we have the actual dispersal distance information after the sequencing occurs, we can easily plug the new information to our general models and create the connectivity maps.

Activity Status as of *January 1, 2019:*

Our Activity 2 goals are right on track. We have created general connectivity models that predict the landscape-level connectivity of species across all grasslands in Minnesota. We worked with Rich Johnson at The Nature Conservancy to get the most accurate GIS layers of all possible grassland types within the state (e.g. native prairies, hay fields, restored prairies, etc). We then used these habitat fragments to make predictions about the connectivity of these fragments using network models for a series of reasonable dispersal distances. This manuscript is currently going around for peer-editing and will be submitted for publication within the next reporting period.

If we receive a Legislative Extension we can update these general models with the dispersal information for our target species and can then provide species specific network-based information on how to conserve these grassland species in Minnesota by understanding their connectivity.

Activity Status as of *July 1, 2019:*

Our general connectivity models for the state of Minnesota are now complete. We have written up a publication of the work which we submitted to Conservation Biology and recently received positive reviews. We are in the process of completing this publication. Once accepted, we will create a 1-page summary to share freely to help managers understand state-wide connectivity. In addition, this work is the basis for our web-based app that we built for Activity 3 (below), which will be available in full for managers this fall.

Activity Status as of *January 1, 2020:*

Activity 2 is complete. Our publication is still in review at Conservation Biology, and we hope that our analysis of the connectivity of grassland fragments of Minnesota will be accepted soon. As mentioned previously, once accepted, we will create a 1-page summary to share freely to help managers understand state-wide connectivity.

Final Report Summary:

Activity 2 is complete. We do still need to create our 1-page summary, but we have published our paper and presented on the connectivity work we created to local land managers.

ACTIVITY 3: Directly inform the MPCP and create conservation connectivity tools

Description: In order to make this project as broadly useful as possible, we will create open-source, user-friendly models that federal and state agency members can use to determine habitat connectivity of many species. We will do this by extrapolating dispersal distance measured in Activity 1 to species that are similar (in terms of dispersal syndrome) to the target species. This information will then be shared specifically with the Minnesota Prairie Conservation Plan in order to provide plant movement information for future re-evaluations of the plan. This information will help determine how big corridors need to be, and how close fragments need to be, in order to maintain plant connectivity. We will make our models available to anyone in a conservation agency that has prairie plant survey data from multiple prairie fragments, and is interested in learning how to prioritize locations for prairie restorations. We will hold virtual workshops to help agency members learn how to use these tools to analyze the connectivity of their landscape. Private land owners interested in restoring prairie can also benefit from this tool and participate in workshops.

Summary Budget Information for Activity 3:

ENRTF Budget:	**$ 13**
Amount Spent:	**$ 13**
Balance:	**$ 0**

Outcome	**Completion Date**
inform Minnesota Prairie Conservation Plan of dispersal distance information	*February 2019*
develop online tools for measuring habitat connectivity	*December 2018*
hold virtual workshops to train agency members, citizens, scholars, etc on how to use the virtual tools to determine connectivity of their own prairie fragments	*May & June 2019*

Activity Status as of *January 1, 2017:*

This activity has not yet begun.

Activity Status as of *July 1, 2017:*

This activity has not yet begun.

Activity Status as of *January 1, 2018:*

This activity has not yet begun.

Activity Status as of *July 1, 2018:*

This activity has not yet begun. However we have hired someone to work on this, and she starts August 1, 2018.

Activity Status as of *January 1, 2019:*

This activity is in full swing and we are meeting our goals. We have developed an online tool for measuring habitat connectivity for all of Minnesota. This is a web-based, interactive app that anyone can use. You select your county, and this brings up all of the grasslands within that county. Then, you have a slider bar to select the dispersal distance you think is appropriate and the application shows you (with connected lines) which prairies are connected to each other based on that dispersal distance and provides a series of connectivity metrics (e.g. the number of connected prairies in your county, the number of isolated prairies, etc). Also, this app allows you to select a location that you think you might want to locate a prairie restoration, and it updates the connectivity metrics to determine if this new prairie will promote connectivity or not given the existing prairies. We have set up meetings in early 2019 to work with the folks from the Minnesota Prairie Conservation Plan to workshop the app to find out what they are interested in and how they think it should be improved to be more useful to managers. After this, we will hold workshops to show anyone who is interested how to use the application.

Activity Status as of *July 1, 2019:*

We have now nearly completed this activity. We have created the web-based app (https://grassland-connectivity.shinyapps.io/MNConnectivity/) that allows managers in Minnesota to examine the grasslands in their county and calculate the connectivity of these grasslands based on given dispersal distances. A web-based tutorial is available to help people understand how to use the the app, and can be found here (https://www.youtube.com/watch?v=bS93mnMyAW8). We will be hosting a web-based seminar for how to use the app this coming fall for managers including the MN DNR, BWSR and others, once field season comes to an end. Additionally, we published a summary paper about the importance of using web-based applications for helping solve conservation management problems in Restoration Ecology, which can be found here (https://onlinelibrary.wiley.com/doi/10.1111/rec.12999).

Activity Status as of *January 1, 2020:*

Due to scheduling conflicts with field work and moving, we have not yet set up our web-based seminar for how to use our app. We are currently working to schedule this workshop.

Final Report Summary:

Activity 3 is complete. Our paper is published and so is the app. We have presented on this work to local land managers.

V. DISSEMINATION:

Description:

Findings from Activities 1 and 2 will be published in peer-reviewed journals. Important findings from these Activities will be shared with parties involved in the project and land managers in Clay County. These bodies include but are not limited to: The Nature Conservancy, The Department of Natural Resources, Fish and Wildlife Services, and Minnesota State University Moorehead. The Minnesota Prairie Conservation Plan will be specifically targeted and all results will be shared and discussed with the founders of this plan.

The online tutorials and connectivity tools created in Activity 3 will be made publicly available to any private citizen, state or federal agency, non-profit, or scientific body interested in the results and methods. Online workshops will be open to any interested party. Contact information will be provided in case users run into snags when using the tools.

Work from Activity 1 and 2 will be presented at the National Native Seed Conference in February 2016 for land managers, policy makers and scientists all interested in promoting the use and production of native seed in the United States.

Status as of *January 1, 2017:*

We have disseminated this research in several ways this reporting period. We presented at the Science Slam for The Nature Conservancy (~ 35 attendees – scientists, TNC staff, and land managers using TNC lands) where we discussed our work to date. We also discussed our project with Minnesota State University Moorhead undergraduate student interns during intern development day (15 students). Here we brought students out to the field site and discussed the project and the conservation-related ideas behind it. Finally, we presented at a monthly meeting for the SNA land stewards run by the Minnesota DNR (6 land stewards). Again, we brought the stewards out to Bluestem Prairie SNA to introduce them to the research that was happening on one of the SNA's.

Status as of *July 1, 2017:*

We have disseminated this research in several ways this reporting period. First, we attended the National Native Seed Conference (~330 attendees – scientists, restoration specialists, policy makers, land managers, native seed producers), where we presented a poster on our work. We received a lot of interest in the project, and made several connections that have helped improve the work of this project. We look forward to sharing our work more as it progresses and we have solid results! We also presented at the MSUM intern development day (7 students) where we talked to students about our research, and our path to become a scientist. We then took the students and other MSUM faculty into the field, showed them our study plots, and had them participate in helping us find individuals of our target species.

Status as of *January 1, 2018:*

Over the past reporting period we have participated in two dissemination events through the Minnesota DNR. First, we contributed to the MN DNR Science Sunday section on their Facebook page. We provided a description of our project, which they published on facebook to inform others about the work occurring in conjunction with the DNR. Also, in September we participated in the MN DNR Little Lunch on the Prairie series, where we presented our project and the results so far via the web to MN DNR land managers across the state. 14 people were in attendance.

Status as of *July 1, 2018:*

During this reporting period Lauren gave a talk at the University of Missouri where she discussed this project and our results thus far. There were approximately 80 people in attendance, including students, faculty and staff. Additionally, Allison gave a talk at the University of Colorado, Boulder where she also discussed the project and its preliminary results. There were approximately 60 people in attendance including students, faculty and staff.

Status as of *January 1, 2019:*

Work from this project has been presented at two University seminars within the last reporting period – one by Lauren at Washington University in St Louis, and one by Allison at St. Olaf. There were approximately 40 ad 30 people in attendance (respectively), and these audiences included faculty and undergraduate students, as well as graduate students at Washington University. This work was also presented at the Ecological Society of America conference in New Orleans in August by both Lauren and technicians Hayley and Katie. Here there were approximately 80 people in attendance – which included ecologists from all around the world.

Status as of *July 1, 2019:*

We beta-tested our web-based app with faculty and students at the University of Minnesota Friday Noon Seminar (~15 people), and with the MN, ND, SD TNC chapter (~10 people). This helped us improve the quality of the app to address questions of interest to managers. Lauren also presented on work from this project (Activities 1 and 2) at the Iowa State University Ecology and Evolution seminar that had approximately 75 people in attendance.

Status as of *January 1, 2020:*

Lauren presented on the general connectivity model at the Ecological Society of America conference in August, 2019. There were approximately 60 people in attendance, all ecologists interested in the concept of connectivity.

Project Results Use and Dissemination

This project has been presented at the Ecological Society of America conference in 2018 to an invited session on the role of space for coexistence as well as in 2019. Additionally, our team presented findings at the Botany Society meetings in 2019, 2020, and 2021 and various intuitional research talks in 2019 and 2020. The list of published papers associated with this project can be found in our Overall Project Outcomes.

One of the main outreach foci of this project was to provide conservation agencies and the MPCP with tools that they can use to determine the degree of habitat connectivity and the necessary size of corridors, to promote the spread of desirable species. To that end, we created and an app to the Nature Conservancy, and the MN DNR in March 2019. This app can be found at MN Connectivity.

VI. PROJECT BUDGET SUMMARY:

A. ENRTF Budget Overview:

See Attached Budget

Explanation of Use of Classified Staff: N/A

Explanation of Capital Expenditures Greater Than $5,000: N/A

Number of Full-time Equivalents (FTE) Directly Funded with this ENRTF Appropriation: 7.25

Number of Full-time Equivalents (FTE) Estimated to Be Funded through Contracts with this ENRTF Appropriation: 0

B. Other Funds:

Source of Funds	$ Amount Proposed	$ Amount Spent	Use of Other Funds
Non-state			
University of Minnesota	$ 289,120	$289,120	In-kind support: non-summer salaries of Shaw and Moeller, office space, lab space
Shaw startup	$1,428	$1428	Two weeks of field work to set up the field sight and begin collecting data before July 1. The flowering season will begin before this date, so it will be necessary to begin before July 1 to get all the appropriate data. Funds include hotel room, per diem and car rental. Details are the same as above.
State			
None			
TOTAL OTHER FUNDS:	**$**	**$**	

VII. PROJECT STRATEGY:

A. Project Partners:

Funded Partners

Lauren Sullivan (Postdoctoral Researcher - UMN) will oversee project and conduct all research, Allison Shaw (Assistant Professor – UMN) will assist with modeling and determining connectivity, and David Moeller (Assistant Professor – UMN) will assist with genetic analysis.

Non-funded Partners

Greg Hoch (MN DNR) and Steve Chaplin (The Nature Conservancy (TNC)) will assist with site selection, promote workshops, and incorporate information gathered into the Minnesota Prairie Conservation Plan to make real change for Minnesota prairies.

We will have many non-funded partners in the Clay County area to broaden the scope of this project. We are working with Brian Wisenden and Tony Bormann at Minnesota State Moorehead (2015 LCCMR grant recipients) to discuss site selection, and outreach opportunities. We will work with them to hire undergraduate field assistants and provide these assistants with research opportunities through the University of Minnesota as well as Minnesota State. We will also provide reciprocal outreach by presenting our work through their outreach program funded by their LCCMR grant. We are working with Brian Winter at the Nature Conservancy, and Cindy Leuth at the Minnesota DNR to get the appropriate permissions to perform our work at the proposed site.

B. Project Impact and Long-term Strategy:

First, this project will provide important data that is now only possible because of cutting edge genetic sequencing technology. This will be the first set of information on the dispersal ability of a suite of species that vary in their dispersal syndromes. This project will provide important conservation information that multiple federal agencies can incorporate into their prairie restoration programs. The connectivity information and ability to measure it will be useful, widely across the state. We have contacted the Minnesota DNR, the Board of Water and Soil Resources, and the Nature Conservancy, and they have indicated that they would be very interested in attending the trainings and that this project would provide important information that would be immediately useful to existing programs. This project is extremely timely because it will increase the success of the Minnesota Prairie Conservation Plan, and will be immediately implemented into its upcoming re-evaluation. This project complements an LCCMR proposal by Daniel Cariveau (UMN) titled "Data driven pollinator conservation" that also seeks to understand habitat connectivity and its importance for native pollinators. We will work with both Cariveau and Crystal Boyd to combine the outreach efforts of our LCCMR projects to bring information about plant movement and their insect pollinators to the general public.

This work will be long-lasting as information will be incorporated into the Minnesota Prairie Conservation Plan. It will also be pivotal for creating precision prairie conservation plans across the state that allow managers to target specific areas for restorations that will help increase prairie habitat connectivity across the state. We anticipate that the data collected in this project could provide the basis for future studies on the dispersal and connectivity of Minnesota prairie species. Where possible, we will seek out collaborations and apply for further funding sources to support this work into the future.

C. Funding History:

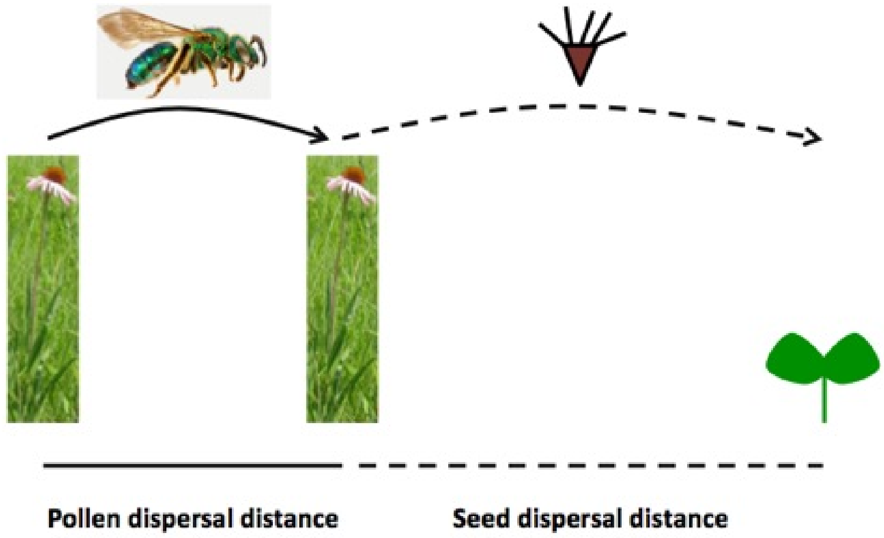
Funding Source and Use of Funds	Funding Timeframe	$ Amount
none		$

VIII. RESEARCH ADDENDUM:
See attached at the end. All published papers are also included.

IX. REPORTING REQUIREMENTS:
Periodic work plan status update reports will be submitted no later than January 1 2017, July 1 2017, January 1 2018, July 1 2018, and January 1 2019. A final report and associated products will be submitted between June 30 and August 15, 2019.

X. VISUAL COMPONENT or MAP(S):

How to measure pollen and seed dispersal distance



Research Area

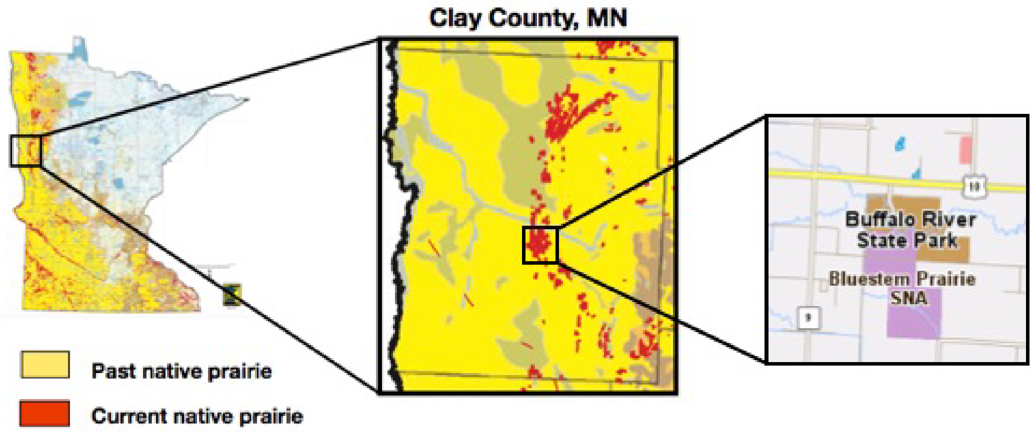
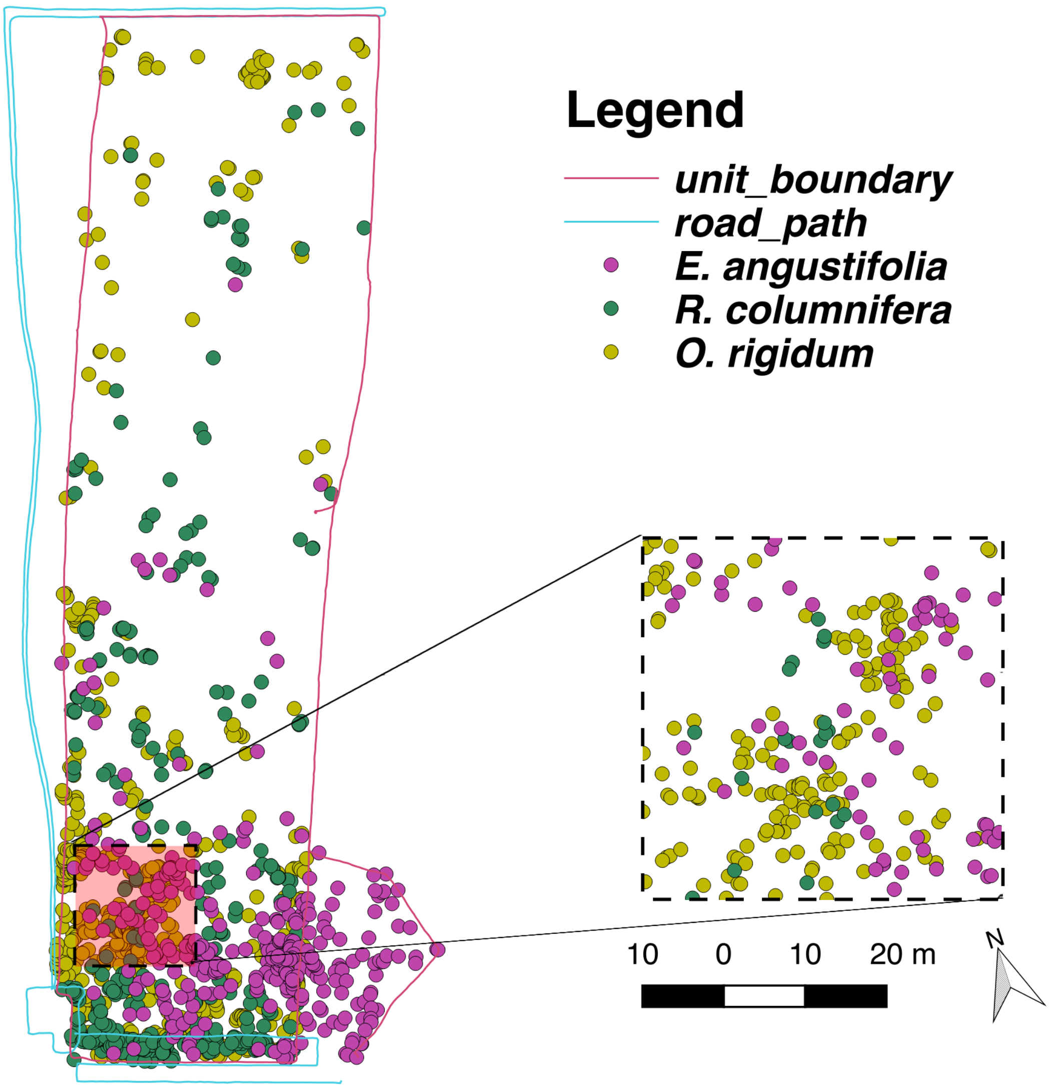


*Image from the Minnesota Prairie Conservation Plan

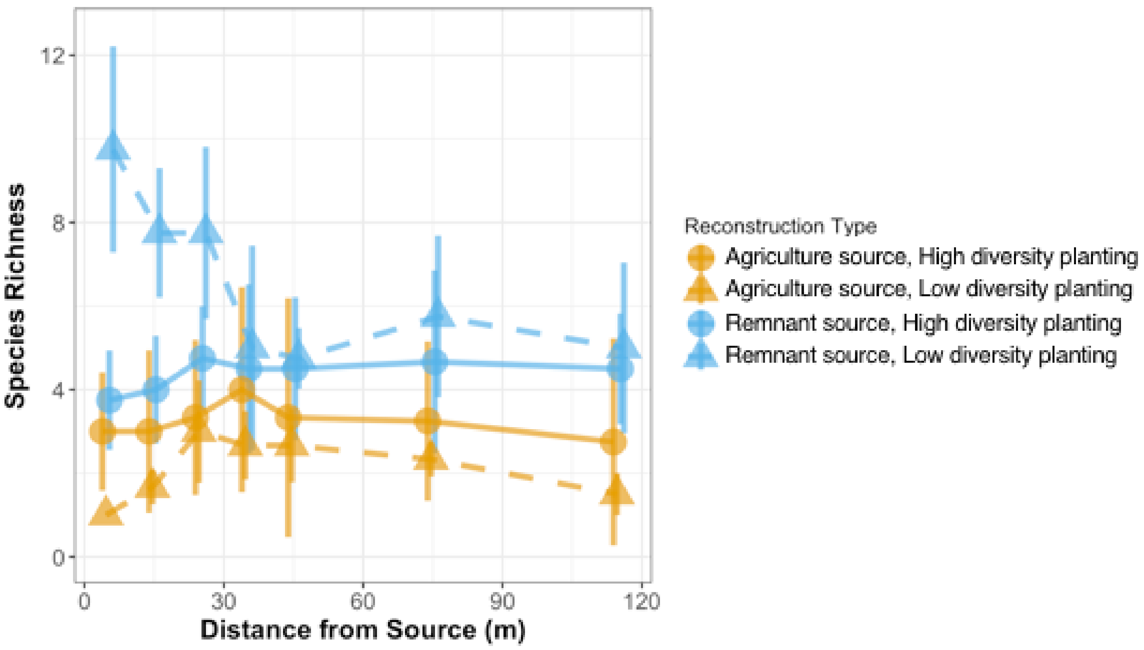
*image from the MN DNR website

Supplemental Figure 1



Supplemental Figure 1: Map of our study area and all individuals of our three target species from 2016. We collected tissue from all individuals of Purple coneflower (*Echinacea angustifolia* – purple circles), Yellow coneflower (*Ratibida columnifera* – green circles), and Stiff goldenrod (*Solidago rigida* – yellow circles) within 3.5 ha at Bluestem Prairie in Clay County, MN.

Supplemental Figure 2



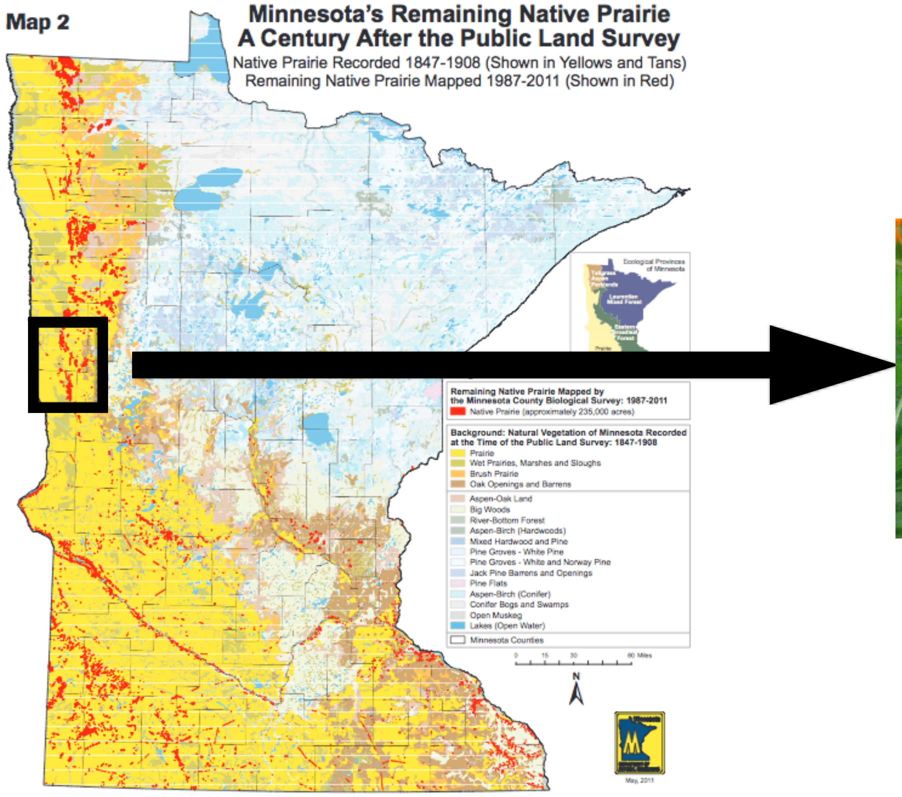
Supplemental Figure 2: Spillover of target species occurred, but only in low diversity reconstructions adjacent to remnant prairies (blue triangles) for the first 50m. There was no significant distance effect for low diversity sites adjacent to agricultural fields (yellow triangles), or high diversity sites adjacent to remnants (blue circles) or agricultural fields (yellow circles).

Environment and Natural Resources Trust Fund
M.L. 2016 Project Budget

Project Title: Measuring Pollen and Seed Dispersal for Prairie Fragment Connectivity
Legal Citation: M.L. 2016, Chp. 186, Sec. 2, Subd. 08b
Project Manager: *Lauren Sullivan*
Organization: University of Minnesota
M.L. 2016 ENRTF Appropriation: $ *556,000*
Project Length and Completion Date: 4 *Years, June 30, 2020*
Date of Report: November 18, 2021

ENVIRONMENT AND NATURAL RESOURCES TRUST FUND BUDGET	**Activity 1 Budget**	**Amount Spent**	**Activity 1 Balance**	**Activity 2 Budget**	**Amount Spent**	**Activity 2 Balance**	**Activity 3 Budget**	**Amount Spent**	**Activity 3 Balance**	**TOTAL BUDGET**	**TOTAL BALANCE**
BUDGET ITEM											
Personnel (Wages and Benefits)	$261,059	$261,059	$0	$138,326	$138,326	$0		$0	$0	$399,385	$0
Lauren Sullivan *UMN postdoc - supervise and participate in the research project full time. 82% salary, 18% benefits. 100% FTE for 3 years ($159,000)*											
Allison Shaw *UMN assistant professor - participate in sampling and develop connectivity models. 75% salary, 25% benefits. 8.333% FTE for 3 years ($36,800)*											
Dave Moeller *UMN assistant professor - participate in sampling and parentage analysis 75% salary, 25% benefits. 8.333% FTE for 3 years ($40,500)*											
*Student field assistants (3 total). 100% salary. 25% FTE for 3 years ($13/hour * 40hr/week * 12 weeks * 3 years = $18,720)*											
Civil Service Tech 1 lab assistant, civil service employee - help with lab work and extractions. 78% salary, 22% benefits.100% FTE for 2 years ($81,580)											
Civil service employee Bioinformatician - assist in data analysis of parentage analysis. 78% salary, 22% benefits. 100% FTE for 1 year ($46,400)											
Equipment/Tools/Supplies											
Field and Lab Supplies (flags, coin envelopes, bar code reader, 96 well plates, chemicals, vials, etc)	$12,000	$12,000	$0	$86	$86	$0				$12,086	$0
GPS Rental	$554	$554	$0							$554	$0
Supplies to conduct workshops (food, name tags, etc)							$0	$0	$0	$0	$0
Printing											
printing materials for workshops							$13	$13	$0	$13	$0
Travel expenses in Minnesota											
Travel for field work *lodging, car rental, per diem.*	$23,788	$23,788	$0	$0	$0	$0				$23,788	$0
Out of state travel for conference to present work from project *(flight: $360 + hotel $900 + registration $400 = $1660)*	$1,660	$1,660	$0							$1,660	$0
Other											

*Lab services for genotyping plant samples to determine paternity (8 species * 250 samples/species the first year, and 4 species * 200 samples/species the second year = 2800 samples @ $50/sample = $140,000*	$118,514	$118,514	$0							$118,514	$0



Measuring pollen and seed dispersal distance

seed dispersal distance

pollen dispersal distance

to determine prairie habitat connectivity and proper corridor size

From: the Minnesota Prairie Conservation Plan

RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

RE-New (Opinion) ARTICLE

Apps can help bridge restoration science and restoration practice

Katie P. Sperry[1,2], Allison K. Shaw[1], Lauren L. Sullivan[1,3]

Scientists need to find innovative ways to communicate their findings with restoration practitioners in an era of global change. Apps are a promising bridge between restoration science and practice because they apply broad scientific concepts to specific situations. For example, habitat connectivity promotes ecological function, but practitioners lack ways to incorporate connectivity into decision-making. We created an app where users calculate how habitat restoration or loss affects connectivity. By providing our app as an example and discussing the benefits and challenges in creating apps for practitioners, we encourage other restoration ecologists to similarly create apps that bridge science with practice.

Key words: digital tools, habitat connectivity, habitat restoration, network analysis, R shiny, web applications

Implications for Practice

- Creating apps can help ecologists present their findings to restoration practitioners.
- When creating apps, it is helpful to communicate with your target audience to understand their needs.
- Not all questions can be answered effectively in apps; it is necessary to understand the scope of your app.

Much of the work we do as restoration ecologists aims to inform restoration practices, and we can take more proactive steps to accomplish this. Scientific studies inherently focus on the big picture by conveying the general consequences of scientific findings. Restoration practitioners, however, often have specific, place-based questions about how these general trends will affect their work. Web applications (or "apps") have the potential to effectively bridge this divide, and, consequentially, they can help us better incorporate cutting-edge restoration science into contemporary restoration practice. By automating analyses and creating user-friendly interfaces, apps can widen the community of people engaging with our work. The usability of apps can help incorporate our findings into restoration practice, therefore increasing the likelihood that our science is used to create more effective restorations. As scientists hoping to affect change with our work, we can aid land managers by creating apps that allow users to interact with and manipulate data within defined parameter ranges. This enables restoration practitioners to engage with new findings in restoration ecology in more meaningful and specific ways because these tools can test the exact scenarios that are relevant to their concerns. Here, we discuss the benefits of creating apps to incorporate restoration science into restoration practice, using our own experience in developing such an app as an example.

One specific issue managers face is deciding where to restore land, as there are often several possible places to conduct restorations. Where we work in the American Midwest, remnant grassland habitat has been highly reduced and fragmented through conversion to agriculture. Ecological theory tells us that this habitat loss and fragmentation has negative consequences for ecological populations and communities because it disrupts connectivity; e.g. through loss of gene flow, population size decline, and decreased movement ability. Connectivity, or the extent to which organisms can disperse between habitat patches on a landscape, can be affected by the decisions we make about where to place restorations or further convert grasslands. Yet, we lack effective tools to translate ecological theory into practical application. Some organizations, such as The Nature Conservancy, do actively prioritize connectivity when planning new restorations. However, many groups that conduct restorations lack the institutional resources to make these kinds of management decisions based on ecological theory. Thus, it is difficult for them to anticipate the impact that restoration or habitat loss would have on connectivity. Further complicating this is the fact that connectivity has many aspects to it, which are each quantified using different metrics. For example, some metrics of connectivity focus on predicting a species' long-range movement ability for coping with climate

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Author contributions: KPS developed the app and wrote the manuscript; KPS, AKS, LLS developed and refined the idea and edited the manuscript.

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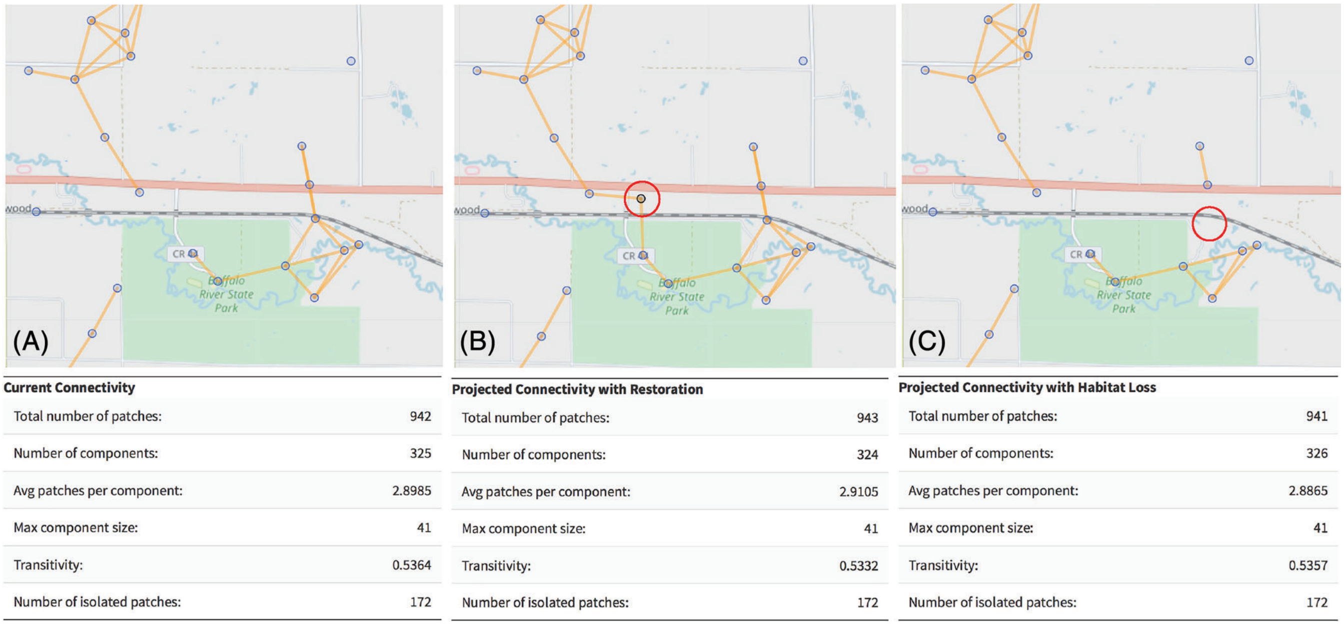

Current Connectivity

Total number of patches:	942
Number of components:	325
Avg patches per component:	2.8985
Max component size:	41
Transitivity:	0.5364
Number of isolated patches:	172

Projected Connectivity with Restoration

Total number of patches:	943
Number of components:	324
Avg patches per component:	2.9105
Max component size:	41
Transitivity:	0.5332
Number of isolated patches:	172

Projected Connectivity with Habitat Loss

Total number of patches:	941
Number of components:	326
Avg patches per component:	2.8865
Max component size:	41
Transitivity:	0.5357
Number of isolated patches:	172

Figure 1. Connectivity app examining different land use scenarios. This view from the app is of a portion of Clay County, MN. Note that connectivity metrics are calculated for the network over the entire county, even though only a portion of the county is shown. (A) Current connectivity. The app calculates and displays the current connectivity in MN counties. Blue circles are the centroids of existing grasslands of at least five acres, and orange lines represent counties that are connected at 1,000 m (defined by the user—not pictured). The data table summarizes the county's current connectivity using several connectivity metrics, which all describe different aspects of connectivity. (B) Projected connectivity with a restoration. When users change the land use scenario to "add" (not pictured) and click on the map, a restoration (black circle, inside the red circle) is added in that location and metrics are recalculated. (C) Projected connectivity with habitat loss. When users change the land use scenario to "loss" (not pictured) and click on an existing patch, that patch is removed (patch's former location marked by red circle) from the networks and metrics are recalculated.

change, while others focus on a species' local recolonization potential. As scientists who study the ecology and math of connectivity, we wanted to create a tool that would allow land managers to easily incorporate connectivity analysis into restoration decisions.

To do this, we created a connectivity app which allows land managers to ask specific questions about habitat connectivity in their region without needing to conduct network analyses (a method used to calculate connectivity) themselves. For example, if a land manager is interested in restoring a tract of marginal cropland into a grassland, they can use the app to quantify how this restoration would impact different aspects of connectivity across the landscape. The app can also be used to quantify the consequences of habitat loss, as many areas continue to lose grassland habitat via conversion to agriculture. Quantitative information on a patch's value to connectivity can be used to help make decisions about where to prioritize restoration or protection.

We created the connectivity app in R Shiny, and it utilizes network analysis to compute the connectivity of grasslands over the state of Minnesota. Users define their landscape of interest by clicking on a county, after which the app shows you the county's grasslands. Because the extent to which a landscape is connected depends on an estimate of how far a species can move, the user has the ability to set the "dispersal distance" from 50 to 2,000 m. Once these parameters—county and dispersal distance—are defined, the app draws connections between grasslands where dispersal is possible at that distance, and also presents the user with a table of metrics describing the connectivity of the created network (Fig. 1). Users can also toggle the land use scenario they are interested in displaying on the interactive map—they can plot the current extent of grasslands in the county, and then can either (1) click to add a grassland on the map (modeling the impact a restoration would have connectivity), or they can (2) click on an existing grassland to remove it (modeling the impact of habitat loss on connectivity). As users add and remove grasslands, they see connections re-forming on the map, and they can compare the county's current connectivity metrics to the projected metrics given these changes on the landscape (Fig. 1). The app addresses our need to maximize future connectivity and protect current connectivity, and to do this effectively we need to be able to anticipate the consequences of restoration or habitat loss in specific locations. With this tool, land managers are better positioned to incorporate connectivity into decisions about where to prioritize restoring or protecting land.

In order to design effective web apps, it is critical to understand the needs of the users. Our target audience for the connectivity app was people and organizations interested in restoring or protecting land. As such, we developed the app with organizations such as The Nature Conservancy, or the Minnesota Department of Natural Resources, as well as private citizens in

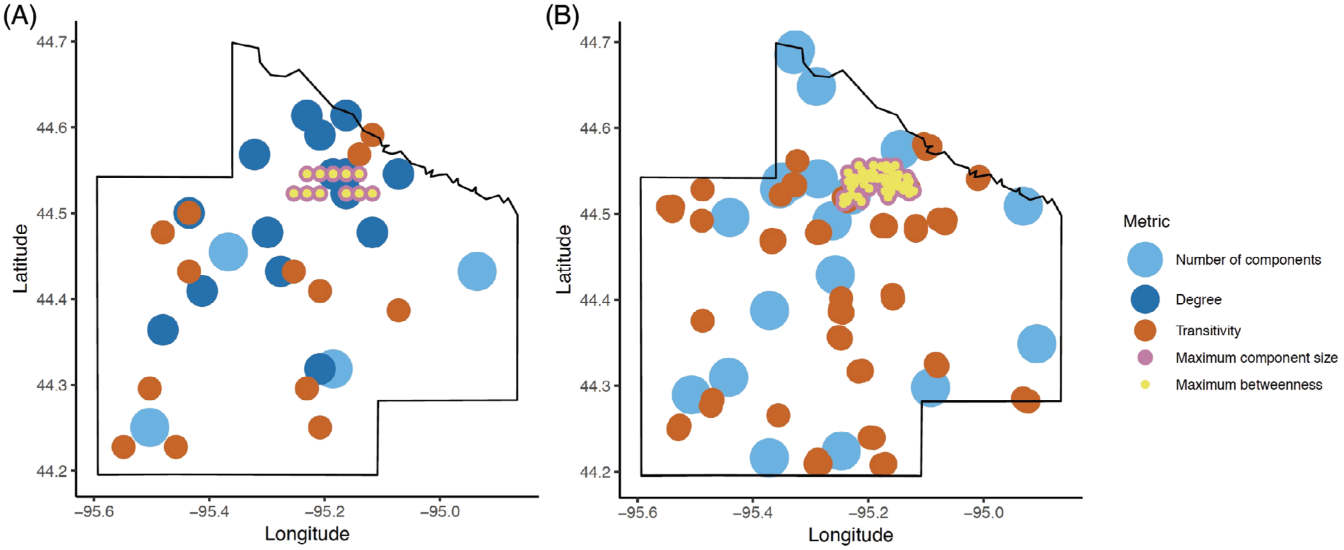

Figure 2. Locations of restoration and habitat loss that most increase and decrease connectivity, respectively. Note: size varies only for visualization purposes. (A) These points represent the locations that, out of all 500 sampled locations, resulted in a network with the optimal outcomes for each metric when they were added to the baseline network, as compared to baseline values. These optimal outcomes are quantified as the top or bottom, depending on which direction is optimal, 5% of all outcomes across the 500 sampled points. (B) These points represent the locations that, out of the 1,235 existing grasslands, resulted in a network with the worst outcome for each metric when they were removed from the baseline network, as compared to baseline values. These worst outcomes are quantified as the top or bottom, depending on which direction is worse, 5% of all outcomes across the 1,235 sampled points (see Appendix S1 for full description).

mind. For us, it was important that we create a tool that enabled people without prior technical experience to assess connectivity. Thus, we prioritized simplicity of the user interface and having informational pages about connectivity. We also wanted to engage with our target audience throughout the development process to make sure we were meeting the needs of the intended users. We gave presentations to our target audience to discuss how we could refine the app. This is a critical step to creating apps that bridge basic and applied science. For example, attendees at our meeting with The Nature Conservancy were interested in anticipating the effects of habitat loss, a direction we had not yet developed. As a result of this conversation, we developed the app's capability to remove grasslands, and the app is now more likely to be helpful in decision-making. This is a good reminder that if we as restoration ecologists want to ensure our work is helpful, we need to truly understand the needs of land managers.

Apps are a promising, innovative way to bridge restoration science and practice, but we need to think about the types of questions that apps can best address. Some analyses do not lend themselves to an app environment because they are too computationally intensive and would take too long to run, leading to a frustrating user experience. However, computational methods within an app can be used to answer these types of questions outside of the app environment. For example, when users tested the app throughout development, they often wanted to know the best place to put a restoration, or the worst place to lose a grassland, in terms of connectivity. These questions are a logical extension of the app but necessitate computing and comparing many hundreds of networks (each with a potential addition or loss). These computations would take hours to complete. To address this problem, however, we realized we could take a function we designed for the app that computes the connectivity metrics of a network and use it in base R to answer these questions. To do this, we (1) computed the resulting connectivity of individually adding hundreds of potential restoration locations to an existing network to find the locations that most maximized connectivity, and (2) computed the resulting connectivity of individually removing each existing grassland (one at a time) from the network to find which locations most decreased connectivity (Fig. 2). We have demonstrated this more complicated analysis with a case study of the grasslands in Redwood County, MN (Supporting Information, Appendix S1). This case study answers an interesting and important question, but one that would not have fit into the scope of our app. Our connectivity app is best used to answer a relatively simple question: What happens to connectivity if a single patch is added or taken away? These more-focused scenarios are better suited to apps, where the user expects output to be displayed promptly.

As restoration ecologists, we can gain a greater perspective of the applicability and efficacy of our science through the process of creating these types of apps. Communicating directly with restoration managers is beneficial for both parties. These conversations and collaborations can help direct our future ecological research, leading us to design studies addressing the gaps in our understanding that managers most need addressed. This will also afford us a better understanding of how our research fits into the process of restoration, helping us to better communicate the broader impacts of our findings and bringing our work to the attention of our target audience more effectively. Habitat restoration will play a key role in ameliorating the erosion of ecosystem functions and services resulting from centuries of habitat degradation and loss. To best do our part as restoration ecologists, we need to actively seek accessible and innovative ways, such as apps, to better communicate our science with those on the ground creating restorations.

Coordinating Editor: Stephen Murphy

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Supporting Information

The following information may be found in the online version of this article:

Appendix S1 Case study of grasslands in Redwood County, MN.

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RESEARCH ARTICLE

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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, & Tscharntke, 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 (Biscoff, 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 & Lindorg, 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

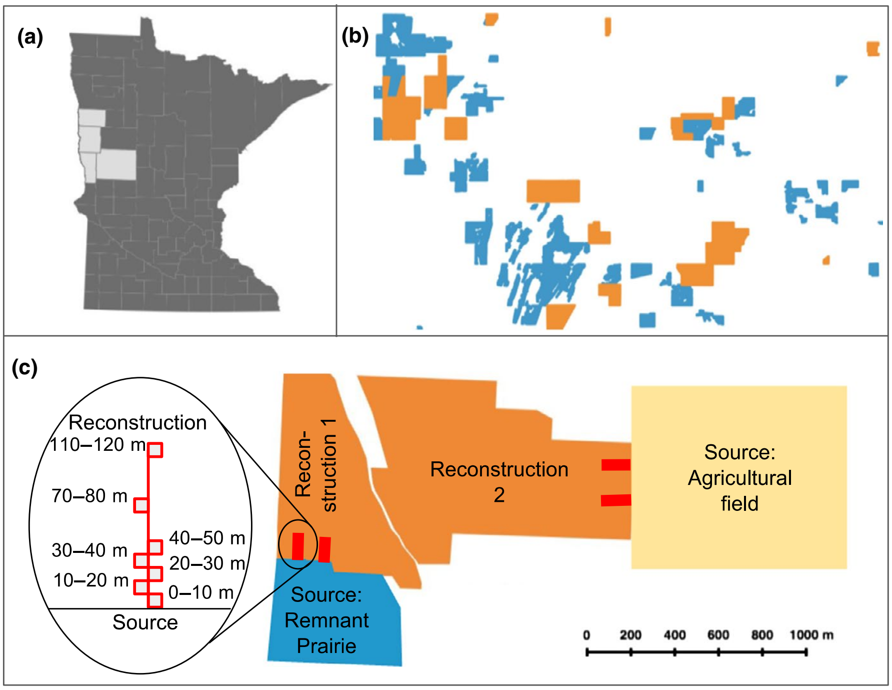

FIGURE 1 Study area and sampling design. (a) Minnesota counties where we conducted surveys are highlighted in light grey: Norman, Clay, Wilkin and Otter Tail. (b) A representational view of the mosaic of remnant (blue) and reconstructed (orange) grasslands. This view is of south-eastern Norman County. (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 though *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 Cornelisson 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 $0.33 \le \times \le 0.78$. An average of 6.6 desirable species spilled

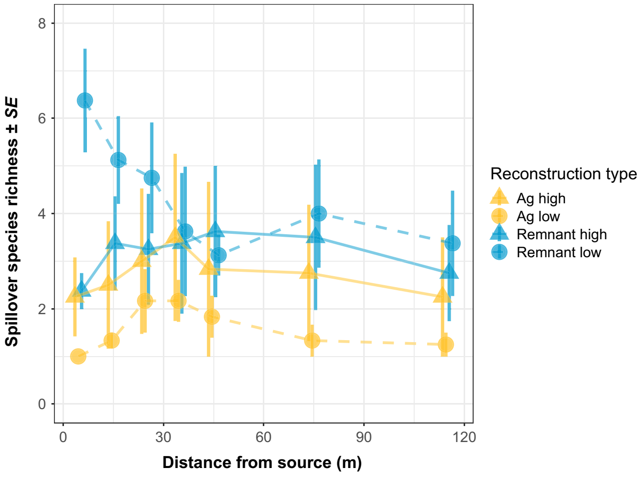

FIGURE 2 Evidence for spillover into reconstructed grasslands. We found evidence for spillover in reconstructions with low species richness adjacent to remnant grasslands (blue circles). In these sites, spillover species richness (desirable, unseeded grassland species) demonstrated a negative relationship 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 *df*	*F* value	*p* 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**

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

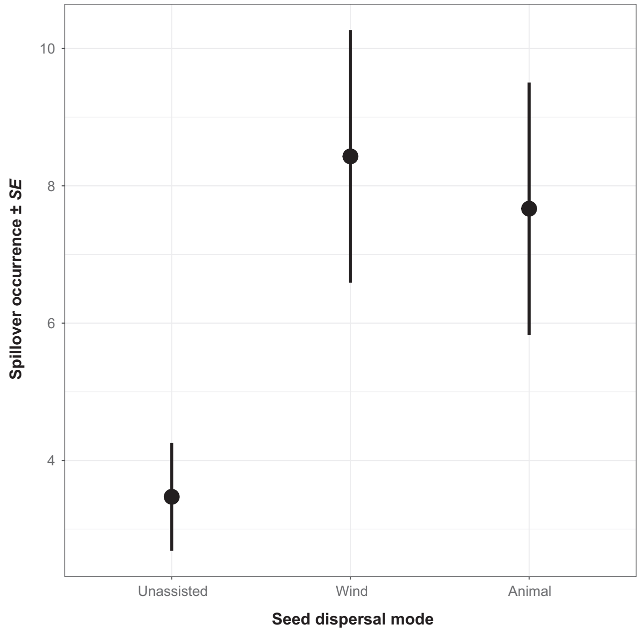

FIGURE 3 Species' seed dispersal mode predicted their spillover occurrence. Based on pairwise comparisons, species with wind dispersed seeds occurred in more plots than species with unassisted seed dispersal, whereas species with animal dispersed seeds trended towards dispersing more than those with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

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, Rouifed, & 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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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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Conservation Biology

Contributed Paper

Consequences of ignoring dispersal variation in network models for landscape connectivity

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Abstract: Habitat loss and fragmentation can negatively influence population persistence and biodiversity, but the effects can be mitigated if species successfully disperse between isolated habitat patches. Network models are the primary tool for quantifying landscape connectivity, yet in practice, an overly simplistic view of species dispersal is applied. These models often ignore individual variation in dispersal ability under the assumption that all individuals move the same fixed distance with equal probability. We developed a modeling approach to address this problem. We incorporated dispersal kernels into network models to determine how individual variation in dispersal alters understanding of landscape-level connectivity and implemented our approach on a fragmented grassland landscape in Minnesota. Ignoring dispersal variation consistently overestimated a population's robustness to local extinctions and underestimated its robustness to local habitat loss. Furthermore, a simplified view of dispersal underestimated the amount of habitat substructure for small populations but overestimated habitat substructure for large populations. Our results demonstrate that considering biologically realistic dispersal alters understanding of landscape connectivity in ecological theory and conservation practice.

Keywords: fragmentation, grasslands, graph theory, network models, population size, weighted networks

Consecuencias de la Omisión de la Variación en la Dispersión en los Modelos de Redes para la Conectividad de Paisajes

Resumen: La pérdida y la fragmentación del hábitat pueden influir negativamente la persistencia de poblaciones y biodiversidad. Sin embargo, estos efectos pueden ser mitigados si las especies tienen una dispersión exitosa entre los fragmentos aislados de hábitat. Los modelos de redes son la herramienta principal para la cuantificación de la conectividad del paisaje, no obstante en la práctica, se tiende a usar una visión excesivamente simplista de la dispersión de especies. Es común que estos modelos ignoren la variación que existe entre individuos en sus habilidades de dispersión y que asuman que todos los individuos se pueden mover la misma distancia y con la misma probabilidad. En este estudio, desarrollamos una estrategia de modelaje para (minimizar o aminorar) estas limitaciones incorporando kernels de dispersión dentro de los modelos de redes para determinar cómo la variación individual de la dispersión altera el entendimiento de la conectividad a nivel de paisaje. Como un ejemplo, implementamos esta estrategia en un paisaje de pastizal fragmentado en Minnesota. Omitir la variación en la dispersión generó una sobreestimación sistemática de la robustez de la población ante las extinciones locales y una subestimación de la robustez ante la pérdida local del hábitat. Además, una visión simplificada de la dispersión subestimó la complejidad de hábitat para las poblaciones pequeñas, sin emgargo sobreestimó la complejidad para las poblaciones grandes. Nuestros resultados demuestran que incorporar parámetros que describan una dispersión

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biológica realista tiene implicaciones importantes en la teoría de conectividad de paisajes e implementación de practicas de conservación.

Palabras Clave: fragmentación, modelos de redes, pastizales, redes ponderadas, tamaño poblacional, teoría de gráficos

摘要: 生境丧失和破碎化会对种群续存和生物多样性产生负面影响, 但如果物种成功扩散到孤立的栖息地斑块, 则可以缓解这种影响。网络模型是量化景观连接度的主要工具, 但在实际应用中, 物种扩散往往被过度简化。这些模型通常假设所有个体以相同的概率移动相同的固定距离, 而忽略了个体扩散能力的变异。本研究开发了一种建模方法来解决这个问题。我们在网络模型中加入了个体扩散函数, 以确定个体扩散能力差异如何改变对景观尺度连接度的理解, 并把我们的方法应用在明尼苏达州的一个破碎化的草原景观中。结果显示, 忽略个体扩散的变异会导致高估种群产生局部灭绝的稳健性, 且低估种群应对局部栖息地丧失能力的稳健性。此外, 简化扩散模型还会低估小种群栖息地亚结构的数量, 并高估大种群栖息地亚结构数量。我们的研究结果表明, 考虑生物学上实际的扩散能力, 可以改变生态学理论和保护实践中对景观连接度的认识。**【翻译: 胡怡思; 审校: 聂永刚】**

关键词: 破碎化, 草地, 图论, 网络模型, 种群大小, 加权网络

Introduction

Loss of habitat is one of the largest anthropogenic threats to Earth's planetary systems (Rockström 2009), and contributes to major declines in biodiversity (Newbold et al. 2016) and other ecosystem services (Haddad et al. 2015). Habitat loss fundamentally alters landscapes by simultaneously decreasing the overall amount of native habitat and changing how the remaining habitat patches are arranged with respect to each other through fragmentation per se (Fahrig 2017). The negative effects of fragmentation (Fletcher et al. 2018) can be mitigated if species are still able to move between physically isolated habitat patches to maintain population connectivity. However, the extent of species' movement among patches remains an open question (Fahrig 2017). Thus, a complete understanding of the degree to which current (Haddad et al. 2015) and ongoing (Wright & Wimberly 2013) fragmentation disrupts connectivity requires accounting for potential species movement among patches.

Recent work examining how organisms move among fragmented patches draws on network modeling (e.g. Saura & Rubio 2010; Fletcher et al. 2013; Ziółkowska et al. 2014; Wimberly et al. 2018). This approach converts spatial data on habitat locations to networks (or graphs), in which nodes represent habitat patches and 2 patches are connected by an edge if organisms can disperse between them (Urban & Keitt 2001). These networks can be analyzed to inform conservation decisions by calculating patch-based or network-based connectivity metrics and by identifying sets of patches that are connected via dispersal and function as a unit (termed *components*). Network modeling has enabled researchers and managers to infer connectivity, identify habitat patches with high conservation value, and quantify the scale of dispersal necessary to maintain connectivity (e.g. O'Brien et al. 2006; Saura & Rubio 2010; Creech et al. 2014). Generally, although models that infer connectivity tend to take into account detailed information about matrix quality between habitat patches and potential ease of flow through this matrix (Moilanen & Hanski 1998; McRae et al. 2008; Wimberly et al. 2018), they are often based on simplistic assumptions about species' movement dynamics. Specifically, network models, particularly unweighted or binary networks that simply consider whether or not patches are connected, tend to define species' dispersal as a single fixed distance, which effectively assumes that all individuals are equally able to disperse up to that distance, but unable to disperse past that distance. Building network models based on the same sets of simplifying assumptions limits one's ability to understand how a broad range of biological factors (such as dispersal behavior) influence connectivity, which is especially problematic because dispersal variation can have many consequences (Snell et al. 2019; Shaw 2020). Simplified dispersal assumptions may over- or underestimate the degree of connectivity or fail to capture important connectivity patterns altogether, thereby preventing accurate estimations of landscape-level habitat use.

An alternative to viewing dispersal as fixed is to account for variation in dispersal, thus more accurately representing movement behavior. Inherent variation among individuals (e.g., sex, personality, body condition), populations (e.g., density), and the environment (e.g., habitat quality, habitat configuration, season) can cause differences in dispersal ability (Snell et al. 2019; Shaw 2020). This dispersal variation can be captured with a dispersal kernel that describes the proportion of individuals traveling any given distance (Shoemaker et al. 2020). Dispersal kernels thus account for variation in distance traveled as well as variation in the proportion of the dispersing population traveling each distance (Kot et al. 1996). In most species, the majority of dispersing individuals travel short distances, remaining close to their source location and thus contributing to local population dynamics (Moles & Westoby 2004). Simultaneously, few individuals move longer distances, and they drive processes like colonization (Soons et al. 2004b), range expansions (Kot et al. 1996), and range shifts (Davis & Shaw 2001). This long-distance dispersal is often defined by the distance traveled by the farthest 1% of individuals (Nathan 2006). Finally, population size can influence dispersal; populations with more dispersing individuals will more fully realize the dispersal kernel and thus be more likely to successfully disperse greater distances. Although network models have the potential to account for variation in dispersal (i.e., via weighted edges [Shanafelt et al. 2017]), most are based either on the assumption of fixed dispersal (e.g. Minor et al. 2009) or have weighted edges to describe how easily an organism can move through a given matrix, ignoring dispersal variation (e.g. Ziółkowska et al. 2014; Wimberly et al. 2018). Those network models that do consider dispersal as a function of distance tend to do so based on simulated draws from dispersal kernels (Fletcher et al. 2011, 2013). Models that more fully explore weighted networks with dispersal kernels allow for a more nuanced representation of species' movement capacity and provide a better understanding of habitat connectivity and the impacts of fragmentation. A deeper understanding of connectivity would influence both the conservation of rare and threatened species that have had natural movement patterns altered by fragmentation, as well as the control of invasive species that are capable dispersers whose movement abilities can be unaltered by fragmentation (Damschen et al. 2008).

We created a series of deterministic network models to understand how variation in dispersal alters estimates of landscape connectivity. We generated networks based on fixed dispersal distances, which allowed us to compare our results with previous studies (e.g., Urban & Keitt 2001; O'Brien et al. 2006; Wimberly et al. 2018). Then, we generated networks based on dispersal kernels, which incorporated variation in dispersal and included the effect of population size. By comparing networks created either with fixed dispersal distances or with dispersal kernels, we explored how variation in dispersal alters understanding of aspects of landscape connectivity, including habitat substructure, robustness to habitat loss, and robustness to local extinction. We sought to provide a starting point for conservation managers interested in understanding how traditional methods might over- or underestimate connectivity based on simplified assumptions about dispersal. We applied these models to fragmented grasslands in Minnesota (Fig. 1), where there is renewed interest from state and local managers to consider connectivity in their restoration efforts. Minnesota managers have created plans for protecting existing grasslands and building future restorations to promote connectivity through the creation of grassland corridors (Minnesota Prairie Plan Working Group 2018), yet these plans were designed with minimal information on species movement because little is known. Thus, Minnesota grasslands are an excellent study system to demonstrate the utility of our broader approach because prior knowledge of, and interest in, connectivity exists and managers there are open to considering how to incorporate more realistic information on species' dispersal into future conservation plans (Minnesota Prairie Plan Working Group 2018; Wimberly et al. 2018; Sperry et al. 2019).

Methods

We created deterministic network models with and without dispersal kernels to draw conclusions about how including biologically meaningful knowledge of dispersal alters predictions about connectivity compared with ignoring dispersal variation. We assumed that dispersal kernels more accurately represent species movement than the assumption of fixed models where all individuals travel all distances with equal likelihood. Our models are general, and thus could apply to any species of interest, including Minnesota grasslands species across a range of dispersal distances, for example, prairie coneflower (*Echinacea angustifolia*, ~9 m) (Ison et al. 2014), ground squirrels (*Citellus tridecemlineatus*, 53–80) (Rongstad 1965), dickcissels (*Spiza americana*, 222 m) (Walk et al. 2004), and burrowing owls (*Athene cunicularia*, 2802 m) (Catlin & Rosenberg 2008) (all are mean dispersal distances).

Habitat Selection

We developed our models for the prairie region of western and southern Minnesota (also called the Prairie Parkland Province). This region was historically grassland but has been fragmented and reduced to ~1% of its original area (Minnesota Prairie Plan Working Group 2018). The spatial locations of the remaining grasslands are well documented and exist in a matrix of mostly agriculture. We refer to each separate grassland fragment as a patch throughout. To build our networks, we used a comprehensive spatial grassland habitat database for the region (The Nature Conservancy 2015). This data set combined the Minnesota Department of Natural Resources' native prairie layer, the U.S. Fish and Wildlife Services' (USFS) Habitat and Population Evaluation Team's (HAPET) 2014 reclassification data set, and the U.S. Department of Agriculture's Cropland Data Layer (CDL) data set. The USFS National Wetlands Inventory layer was used for corrections in classifying wetland and open water areas. The resulting database consisted of all grassland types, including native remnant prairie, reconstructed or disturbed grasslands, and hay or pasture fields. We included all of these grassland types in our network analysis because

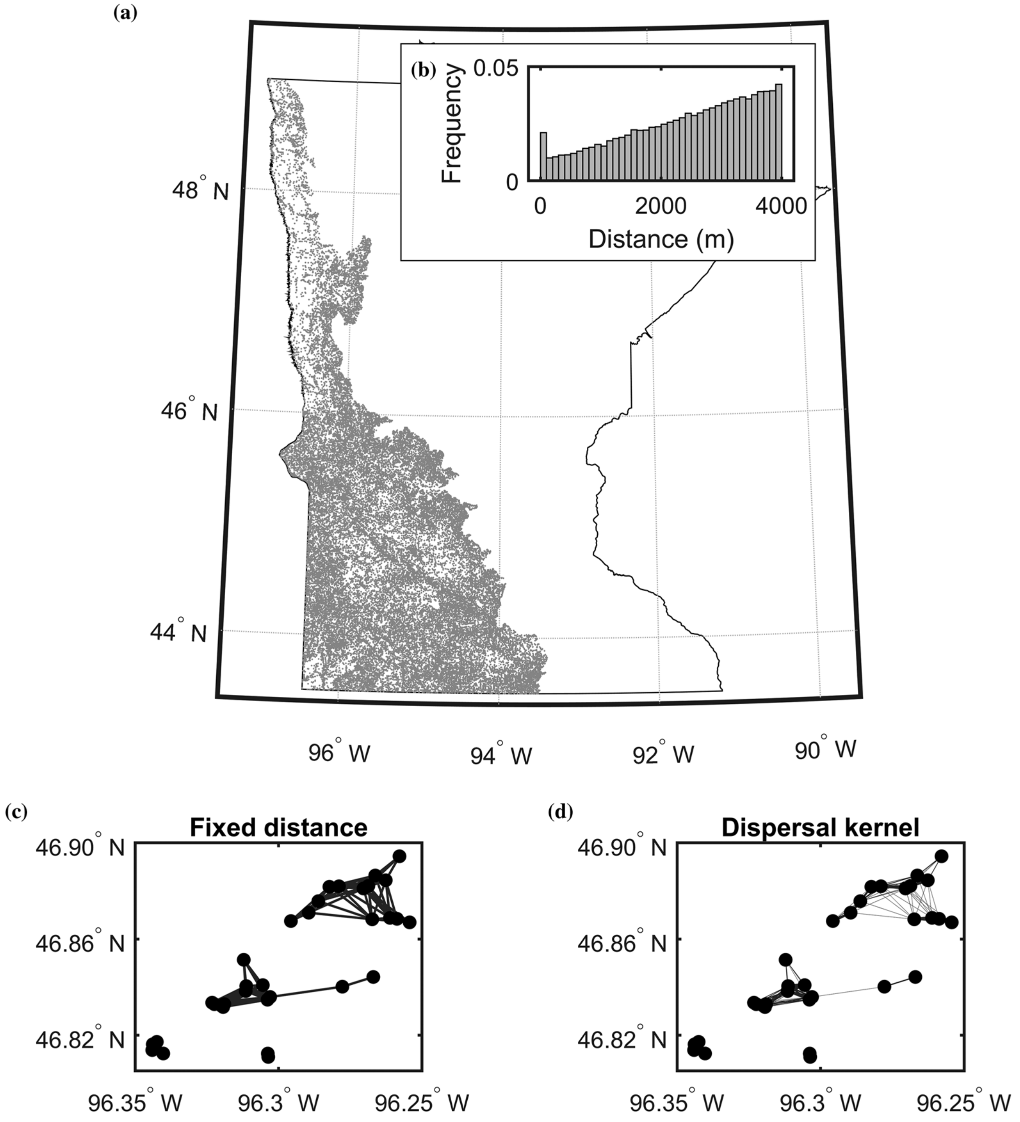
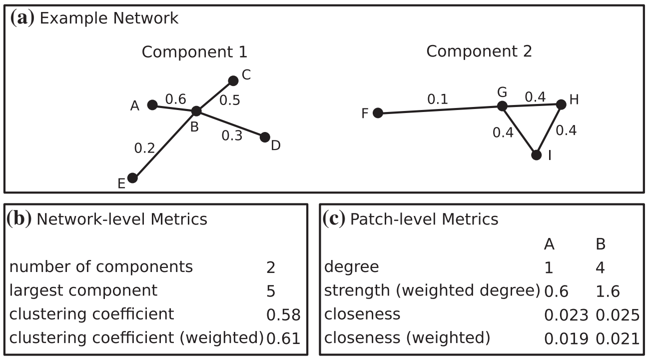


Figure 1. (a) Locations of the ∼37,000 grassland patches across Minnesota (U.S.A.) used in the analysis of dispersal networks, (b) distances between habitat patches up to 4000 m (maximum in models examined), and examples of a subset of the network (Clay County) showing patches and connections under (c) a fixed distance ($d' = 2000$) *and (d) dispersal kernel* ($d^* = 2000$ *and 99%-realized dispersal kernel). In (d) thicker lines correspond to a higher proportion of dispersers between patches.*

they represent potential habitat for grassland species (e.g. birds, insects, mammals, plants). Similar to Wimberley et al. (2018), we used ArcGIS 10.4 to select patches that were 2.023 ha (5 acres) or larger. This resulted in ∼37,000 grasslands ($N = 37,091$ patches in the network, see Appendix S1 for all parameters) to use in our connectivity analysis (Fig. 1a,b).

Networks Based on Fixed Dispersal Distances

We generated networks for our grasslands based on the assumption that organisms had no dispersal variation (i.e., all individuals traveled a fixed dispersal distance). To do this, we calculated the nearest-edge distance (i.e., the distance between the closest points) of all pairs of patches in ArcGIS with the geodesic method and set a maximum search radius of 4000m (Fig. 1c). We chose this radius, which is within the range used in similar studies (Wimberly et al. 2018), for computational simplification, but note that it is smaller than the movement ability of extremely vagile Minnesota grassland species (e.g. the red fox [*Vulpes vulpes*] disperses on average ∼31,000 m [Storm et al. 1976]). We then generated 2000 networks, 1 for each fixed dispersal distance (d') that we considered (1, …, 2000 m). For each dispersal distance d, we generated a binary adjacency matrix $\mathbf{A}$ (of size $N \times N$) in which each element described whether (1) or not (0) the distance between a pair of patches was $<= d$ (i.e., whether



(b) Network-level Metrics

number of components	2
largest component	5
clustering coefficient	0.58
clustering coefficient (weighted)	0.61

(c) Patch-level Metrics

	A	B
degree	1	4
strength (weighted degree)	0.6	1.6
closeness	0.023	0.025
closeness (weighted)	0.019	0.021

Figure 2. (a) Toy dispersal network with 9 patches (A-I) and 2 components (Numbers along edges indicate probability that 2 patches are connected via dispersal and are used to calculate weighted metrics. When calculating nonweighted metrics, probability values become 1.); (b) network-level metrics calculated for the network in (a) (Only nodes B, G, H, and I are used for these calculations because the clustering coefficient only counts nodes with degree >1); and (c) patch-level metrics as calculated for 2 example patches (A and B in component 1).

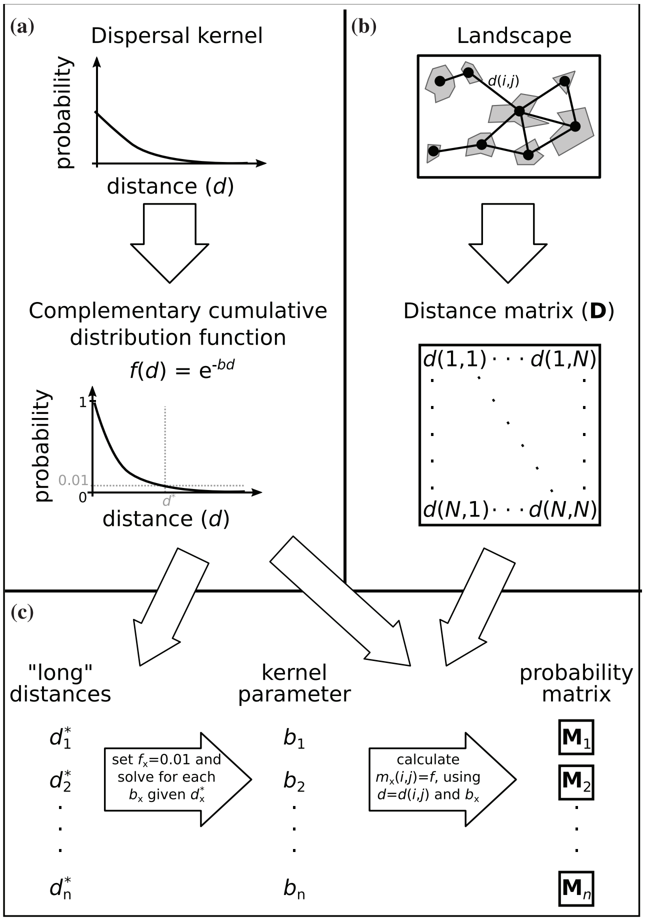


Figure 3. Schematic for building networks from dispersal kernels: (a) dispersal kernel (proportion of population traveling a distance d*) used to calculate the complementary cumulative density function (CCDF) (*f*, proportion of individuals traveling a distance* d *or more;* d**, *long-distance dispersal – [1%] individuals traveling* d *or more); (b) landscape of* N *patches used to calculate the physical distance between all pairs of patches* i *and* j *(i.e., distance matrix [**D**]); and (c) the deterministic map from each long distance (d_x*) to corresponding dispersal kernel parameter (b_x) (caculated by setting f_x to 0.01) and then to the weighted matrix (**M_x**, proportion of individuals dispersing between all pairs of patches* i *and* j*) (using* f *and **D**), where* x *is the dispersal distance index* x *= 1,…,*n *(*n *= 2000). See Appendix S1 for full definitions of parameters.*

an individual traveling that distance could move between these 2 patches). This generated 2000 binary adjacency matrices **A** (of size N x N) in which each element described whether (1) or not (0) 2 patches were connected for each dispersal distance. We then used each matrix to create a nondirected network in the igraph package in R (Csardi & Nepusz 2006). To guide readers through our methods, we also created a toy network (Fig. 2a).

Networks Based on Dispersal Kernels

We also generated networks for our grasslands assuming that individual organisms varied in their dispersal ability (i.e. their movement was described by a dispersal kernel [Fig. 1d]). Specifically, we used the exponential distribution (Fig. 3a) in which the proportion of individuals traveling any distance d is

$$e^{-bd}, \tag{1}$$

where b is the rate parameter. This distribution is commonly used as a dispersal kernel because it often matches empirical data (Hovestadt et al. 2011; Shaw et al. 2019). As with the fixed distance networks, we also considered 2000 dispersal distances. However instead of considering these to be the exact distances traveled, we considered these to be the farthest 1% value (d^*) for defining long-distance dispersal for our dispersal kernels. Thus we established a dispersal kernel for each $d_x{}^*$ value ($x = 1, \ldots, 2000$ m) as follows. We determined the proportion of individual dispersing each distance d or more, given by the complementary cumulative distribution function (CCDF) for the exponential kernel (Fig. 3a). We set this proportion f to be 0.01, plugged in each $d_x{}^*$, and solved for the corresponding b_x value (Fig. 3c), that is

$$b_x = \frac{-\ln(0.01)}{d_x^*}. \tag{2}$$

This b_x value describes a dispersal kernel for which only 1% of individuals dispersed a distance of d_x^* or farther. Next, we calculated the nearest-edge distance between all pairs of patches up to a maximum distance of 4000 m, resulting in a Euclidian distance matrix, **D** (Fig. 3b). Setting a maximum distance for these calculations (rather than calculating all pairwise distances) saved computational time while ensuring we calculated all relevant distances needed for our kernels below. Finally, for each dispersal distance d_x^* we converted the distance matrix, **D**, into a matrix $\mathbf{M}_x$ to describe the proportion of the modeled population that disperses between each patch (Fig. 3c). To do this, for each d_x^* value, we used the CCDF to calculate the proportion of individuals $m(i,j)$ with dispersal kernel defined by b_x that would travel at least the distance $d(i,j)$ between each patch i and j. We then used these $\mathbf{M}_x$ matrices to generate weighted nondirected networks in which the weight of each edge corresponded to the proportion of dispersing individuals that could move between the 2 patches the edge connected.

Finally, we explored the influence of population size on connectivity metrics. A dispersal kernel describes the distribution of distances that would be observed across a very large number of dispersal events. However, because species vary in population size and fecundity, they will also vary in how well the kernel is realized . These differences will appear most strongly for the low-probability long distances (the dispersal kernel tail). A species with a small population size or low fecundity will have few realized dispersal events and thus across the population there will be few dispersal distances represented by the tail of the kernel. To mimic different population sizes with our models, we set the **M** threshold at 3 values by keeping the 75% (all dispersal probabilities < 25% set to 0, i.e., 75% realized, a small population), 99% (99% realized, medium population), and 99.99% (99.99% realized, large population) highest dispersing proportion. This is equivalent to truncating the dispersal kernel at 3 increasingly long maximum distances, but does not incorporate uncertainty and represents the simplifying assumption that small populations are less likely to reach longer distances than large populations. Imposing a maximum dispersal distance also kept the dispersal kernel from becoming infinite (i.e., there is a very small proportion of individuals dispersing infinitely far). An alternative approach to examining population size is to multiply all weighted edges within the network by these proportions (0.9999 for large populations, 0.99 for medium populations, 0.75 for small populations) and then conduct network analyses. This approach leads to qualitatively similar results for patch-level metrics to those we present here (Appendix S2).

In total, we considered 2000 different measures of long-distance dispersal and 3 different measures of population size, generating 6000 weighted networks. As above, we calculated network and patch-level metrics for each network, some of which were modified to accommodate the weighted network structure.

Network-Level Connectivity Metrics

For each network generated with fixed dispersal (nonweighted) and dispersal kernels (weighted), we calculated 3 network-level metrics (Fig. 2b) to quantify different aspects of network structure and connectivity. The first 2 metrics (number of components and maximum component size) do not take into account weights and thus were calculated the same way for both nonweighted (binary) and weighted networks. For number of components (see Appendix S3 for igraph functions), 2 patches were in the same component if they were connected by an edge; fully isolated patches were their own component. Patches in different components were isolated from each other; thus, the number of separate components in a network provided a rough sense of overall fragmentation across the network (Calabrese & Fagan 2004). For maximum component size, the number of patches in the largest component of the network provided a measure of effective network size (Urban & Keitt 2001). Both the number of components and the size of the largest component represented an estimate of the amount of habitat substructure present. Average clustering coefficient quantifies the extent to which a network contains well-connected clusters of patches and thus provides an estimate of local landscape connectivity. In nonweighted networks, for a given patch i that is connected to k_i neighboring patches (see patch-level metrics below), there can be at most

$$\left(1/2\right) k_i(k_i - 1) \tag{3}$$

connections among its neighboring patches. The clustering coefficient for this patch is the fraction of those possible connections that actually occur (Watts & Strogatz 1998), a metric used to quantify the local connectivity for landscape networks (Wimberly et al. 2018). Average clustering coefficient can be considered a measure of robustness to habitat loss because networks with higher clustering will more easily maintain their substructure even as habitat fragmentation removes either edges or patches. For weighted networks, we used weighted distances between patches based on dispersal proportion (Csardi & Nepusz 2006). This weighted clustering coefficient is calculated as

$$\frac{1}{s_i\left(k_i - 1\right)} \sum_{j,h} \left\{ \frac{1}{2} \left[m\left(i, j\right) + m\left(i, h\right) \right] a\left(i, j\right) a\left(i, h\right) a\left(j, h\right) \right\}, \tag{4}$$

where s_i is the strength of patch i (see below), k_i is the degree of patch i, $m(i,j)$ are the elements of the weighted matrix **M**, and $a(i,j)$ are the elements of the adjacency matrix **A**. There was little difference between the mean and median values for clustering coefficient, except for small to moderate dispersal distances in the 75%-realized kernels where the mean value was larger than the median value (Appendix S4).

Patch-Level Connectivity Metrics

For each patch within each network, we also calculated 2 patch-level metrics (degree and closeness centrality) (Fig. 2c) and summarized them by looking at the 25th, 50th, and 75th quantiles of all values for patches within each network. For nonweighted networks, degree centrality was calculated as the number of connected neighbors each patch has (k_i), that is, the number of patches that an individual could potentially reach via dispersal as defined by the model (Wimberly et al. 2018). For weighted networks we calculated strength, the weighted version of degree centrality, as

$$s_i = \sum_j m\left(i, j\right), \qquad (5)$$

where $m(i,j)$ are the elements of the weighted matrix $\mathbf{M}$ for all connected neighbors j of patch i.

Degree centrality or strength quantifies the number of colonization opportunities to or from each patch and represents a measure of short-term robustness to local (patch-level) extinction. Patches with low degree or strength are likely to be isolated and vulnerable to reductions in species richness because any local extinction would be unlikely to be recovered by recolonization from other patches. For nonweighted networks, closeness centrality quantifies the importance of each patch i for overall connectivity in the network as

$$\frac{1}{\sum_{i\neq j} p_{ij}} \qquad (6)$$

where p_{ij} is the shortest path or the number of steps (i.e., sequential dispersal events) it takes to reach every other patch j in the network from the focal patch. If 2 patches are not connected (i.e., p_{ij} is infinite), the total number of patches (N) is used instead of p_{ij} for this pair. Thus closeness is a measure of the average number of sequential dispersal events required to recolonize the network and represents a measure of long-term robustness to local extinction. We chose closeness as our centrality metric (rather than betweenness as used by Minor & Urban [2007]) because closeness more accurately represents dispersing organisms that do not always take the most efficient route between patches (Borgatti 2005). For weighted networks, we calculated a weighted version of closeness, as

$$\frac{1}{\sum_{i\neq j} q_{ij}}, \qquad (7)$$

where q_{ij} is the sum of inverse probabilities m^{-1} along the shortest path between patch i and patch j. Because the inverse of the proportion of dispersers gives an expected number of events needed (e.g., a 0.5 proportion of dispersers would take about 2 dispersal events), weighted closeness is again a measure of long-term robustness to local extinction because it tallies the expected number of sequential dispersal events required to recolonize the entire network. As for nonweighted networks, if 2 patches are not connected, the total number of patches (N) is used instead of q_{ij} for that pair. This correction for unconnected patches (while a suitable approximation for nonweighted networks) is actually an underestimate of the number of sequential dispersal events for weighted networks. Because the degree to which it underestimates dispersal events (and thus overestimates weighted closeness) interacts with the different population sizes we considered, there is no meaningful way to compare across different truncations of the dispersal kernels for this metric. Thus, we only calculated weighted clustering coefficient for the networks based on the 99%-realized dispersal kernels.

All analyses were run in R 3.4.4 (R Core Team 2017).

Results

Network-Level Metrics

Networks were less fragmented (i.e., had less habitat substructure) for large dispersal distances, resulting in fewer components (Fig. 4a) and larger largest components (Fig. 4b). These relationships were starkest for networks created from dispersal kernels with long realized kernel tails (i.e. large population size or high fecundity). In other words, the 99.99%-realized kernel showed the fastest drop in the number of components and the fastest increase in size of the largest component with increasing d^*, whereas the 75%-realized dispersal kernel showed a markedly slower decrease in the number of components and slower increase in maximum component size with increasing d^*. The fixed dispersal distance produced accurate estimates for populations of intermediate size (the 99%-realized dispersal kernel) (Fig. 4a & b). Intuitively, this result occurs because a network from a fixed dispersal distance of d' is structurally equivalent to a network with a 99%-realized dispersal kernel with distance d^* (the same patches are connected in both when considering nonweighted [or binary] network metrics such as the number of components and largest component size). However, fixed dispersal distance underestimated habitat substructure for smaller populations (75% realized) and overestimated habitat substructure for larger populations (99.99% realized).

Networks were also more connected for larger dispersal distances; they had higher clustering coefficients (Fig. 4c). In other words, populations with larger dispersal distances were more robust to habitat loss leading to

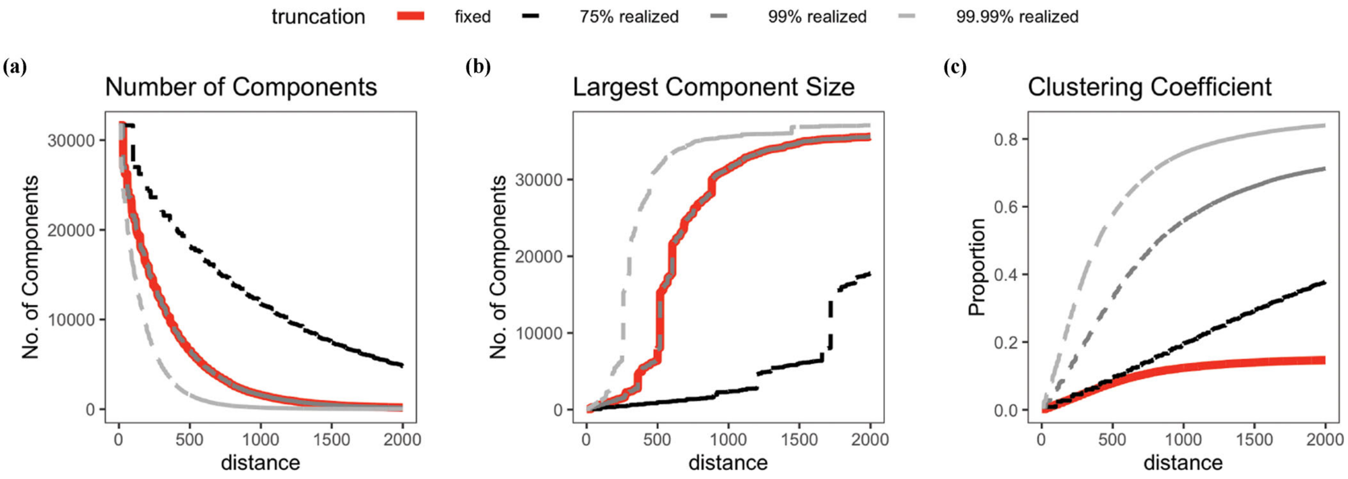


Figure 4. Network-level metric values for networks with fixed dispersal distances (red) and with the exponential dispersal kernel at different tail truncations, 75% realized (dark gray), 99% realized (medium gray), and 99.99% realized (light gray), which represent increasing abilities for long-distance dispersal: (a) number of components, (b) size of the largest component, which represent measures of habitat substructure, and (c) clustering coefficient, which represents robustness to habitat loss.

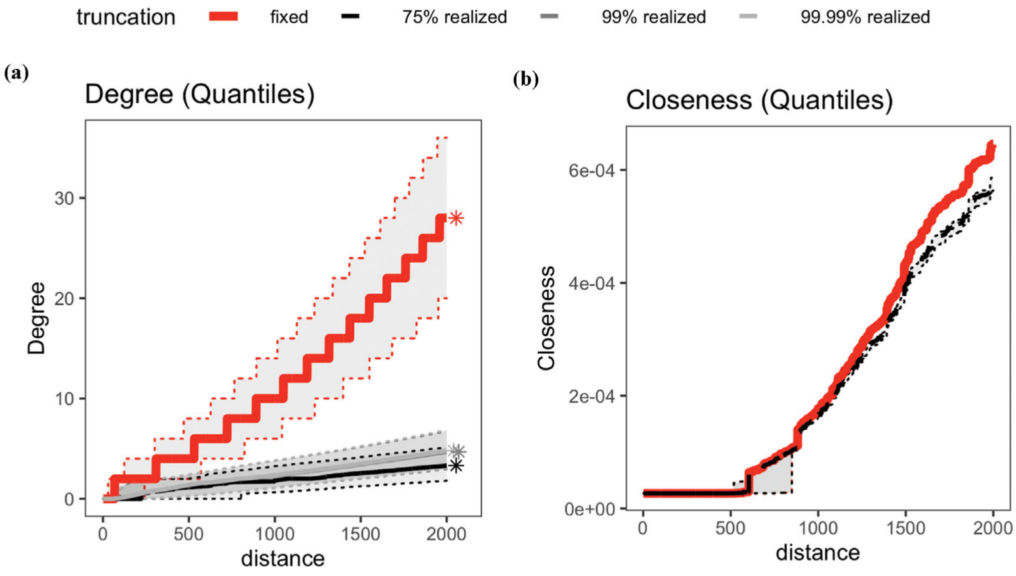


Figure 5. Patch-level metric values for networks with fixed dispersal distances (red) and networks with different dispersal kernels, 75% realized (dark gray), 99% realized (medium gray), and 99.99% realized (light gray). Panels show the 25th, 50th (asterisks), and 75th quantiles for (a) patch degree centrality and (b) patch closeness, which are measures of robustness to local extinction. In (a) 99%-realized kernel and 99.99%-realized kernel nearly overlap with 99.99%-realized kernel, which has a slightly higher degree.

lost patches or connections. However, the fixed dispersal distance consistently underestimated robustness to habitat loss compared with all 3 populations sizes (75%-, 99%-, 99.99%-realized dispersal kernels) (Fig. 4c). The largest difference occurred for the largest population sizes (99.99%-realized kernel). The fixed network and the 75%-realized kernel produced similar results for low dispersal distances, but the clustering coefficient then plateaued for the fixed distance, whereas the 75%-realized kernel continued to increase for large dispersal distances.

Patch-Level Metrics

Patches in networks with large dispersal distances were on average connected to more neighbor patches (higher degree centrality) (Fig. 5a) and represented a high short-term robustness to local extinctions. Networks from fixed dispersal distances consistently overpredicted robustness compared with networks from dispersal kernels, a gap that increased with dispersal distance. In other words, fixed kernel networks systematically overpredicted the number of neighbors (and thus expected number of recolonization opportunities) each patch had compared with dispersal kernel networks. Within the dispersal kernel networks, the smallest populations (75%-realized kernel) had patches with the lowest robustness, followed by medium (99%-realized kernal) and large (99.99%-realized kernal) population sizes. However, these ranges overlapped substantially. Similarly, patches in networks with large dispersal distances had high closeness values (Fig. 5b). Fixed dispersal distances consistently overpredicted closeness and thus underpredicted the number of sequential dispersal events needed to recolonize a network following extinction, compared with the networks created with dispersal kernels.

Discussion

We built deterministic network models from fixed dispersal distances and dispersal kernels, and contrasted them to more fully explore how weighted networks that use dispersal kernels affect estimates of landscape connectivity. As with other simulation-based connectivity models that incorporate dispersal variation (Palmer et al. 2014), we found that network models based on dispersal kernels generated a markedly different understanding of population connectivity than network models based on a fixed dispersal distance (Figs. 4–5, Appendix S5). Specifically, using fixed dispersal consistently overestimated a population's robustness to local extinctions while underestimating robustness to habitat fragmentation. Our results from fixed dispersal distances qualitatively matched similar network analyses for other grasslands (Wimberly et al. 2018) and for forests (Urban & Keitt 2001), suggesting that current habitat management based on fixed dispersal networks is applying inaccurate estimates of population connectivity. Because there is ample evidence that most organisms have substantial variation in dispersal (e.g. Baguette 2003; Krkošek et al. 2007; Sullivan et al. 2018), connectivity models must account for such variation by using dispersal kernels. Other network models that use dispersal kernels to match empirical movement data show these methods to be a good approximation of movement ability (Fletcher et al. 2011, 2013). These findings have implications for managers who plan for conservation based on connectivity metrics. Some species of concern may need more total habitat, whereas others rely on continual recolonization and thus would differ in whether fixed models over- or underestimated their connectivity.

The magnitude of differences between fixed and dispersal kernel connectivity metrics depended on how we modeled the tail of the dispersal kernel, which reflected a examining different population sizes of organisms. The underestimate of robustness to habitat fragmentation (clustering) was the largest for large populations (99.99%-realized dispersal kernel) (Fig. 4c). In contrast, the overestimate of robustness to local extinction (degree centrality) was similar for all population sizes, but slightly larger for small populations (75%-realized dispersal kernel) (Fig. 5a). Degree centrality estimates the expected number of patches that can be colonized with a single set of dispersal events. Because fixed dispersal is effectively based on the assumption of perfect dispersal (patches within a fixed distance will always be reached), networks with fixed dispersal will always overestimate colonization ability.

In light of our results, explicit consideration of conservation goals can help guide the appropriate use of dispersal kernels for management and planning. Inherent in the use of dispersal kernels is the understanding that most individuals move short distances and few individuals move far. Therefore, the conservation goals at the heart of maintaining connectivity should take population size into account when appropriate. For example, often the goal of promoting connectivity between patches is to build a functioning metapopulation for rare species where individuals can move freely and breed between patches (Hanski 1998). Because rare or threatened species are often dispersal limited due to small population sizes and low fecundity (Baur 2014), considering a less realized dispersal kernel (i.e., 75% realized) could more accurately represent likely connectivity outcomes for this particular goal. Moreover, if small population sizes are of serious concern, other methods might need to be incorporated, including individual based models (Grimm & Railsback 2005). Another goal of maintaining connectivity may be to allow for the possibility of species' response to climate change via range shifts (Krosby et al. 2010). Range expansions often proceed through the dispersal of a few individuals over a long distance (Davis & Shaw 2001). To successfully track climate change, large populations must produce the few individuals that disperse long distances; thus, a more realized dispersal kernel (i.e., 99.99% realized) would be more appropriate to include in network models to achieve this goal. Consideration of these highly realized dispersal kernels is also appropriate for controlling invasive species, such as the cane toad (*Rhinella marina*), that have high movement ability (Perkins et al. 2013). Finally, for sessile organisms such as plants, managers may be interested in distinguishing between maintaining high genetic diversity to decrease the probability of inbreeding depression—which requires the movement of gametes (i.e., pollen)—versus allowing for species recolonization to increase species diversity—

which requires the movement of individuals (i.e. seeds) (Elistrand 1992; Brudvig et al. 2009). In this case, managers should consider defining dispersal kernels that represent pollen and seed dispersal separately in order to match their management goals. When looking to define dispersal kernels, managers can use measurement-based (e.g., Stevens et al. 2010), trait-based (e.g., Soons et al. 2004a), or genetic-based approaches (e.g., Bacles et al. 2006) to estimate kernels.

Grasslands are globally important, yet they are among the most threatened due to land-use conversion and fragmentation (Soons et al. 2005; Newbold et al. 2016). Our network models help elucidate how likely species are able to move between grassland patches and maintain connectivity at a broader scale. Our results are comparable to those of Wimberly et al. (2018), who determined connectivity of the grasslands in the Prairie Coteau region of Minnesota and the Dakotas, but used a fixed dispersal distance. Extrapolating their results based on our findings from network models with dispersal kernels, one might expect that for species with large population sizes there may be increased connectivity, with fewer, larger components that are more robust to fragmentation than what Wimberly et al. (2018) found. One might expect the opposite for species with small populations. To aid Minnesota grassland managers, we created a web-based app to allow for the direct application of network models to existing grasslands in Minnesota (Sperry et al. 2019). This approach could be easily updated to incorporate known dispersal kernel information for species of interest (e.g., grassland plant species [Sullivan et al. 2018]), patch prioritization, or matrix quality between patches (Castillo et al. 2016), which would afford a more targeted understanding of which species can maintain connectivity and which may require assistance moving between patches.

To determine whether and where connectivity is maintained between isolated habitat fragments, one must account for how organisms move in a biologically meaningful way. We took steps toward this goal by considering variability in dispersal in network models by incorporating fully explored dispersal kernels to determine how this alters the view of network-based connectivity relative to standard methods that are based on a fixed dispersal distance. Because interspecific dispersal variation is also common, future work should examine how dispersal varies across species (e.g., when different species have different dispersal kernel shapes) and when there is directionality in dispersal to understand more fully how interspecific variation affects connectivity. We found that models ignoring dispersal variation simultaneously overestimated robustness to local extinctions while underestimating robustness to habitat loss, relative to models that accounted for dispersal variation. The magnitude of these differences depends on both biological traits of the species of interest, particularly population size, and dispersal distance.

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Supporting Information

Additional information is available online in the Supporting Information section at the end of the online article. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author. Data and code are available at the Zenodo Digital Repository https://zenodo.org/record/4279644#.X7VYcFlMG3d.

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