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RESEARCH ARTICLE

Connectivity measures across scales differentially influence dryland sediment and seed movement

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Drylands makeup over 40% of the terrestrial land surface area and are highly vulnerable to degradation. The drivers of dryland degradation can lead to shifts in vegetation, such as woody plant encroachment into historic arid grasslands. Encroachment often creates connected bare plant interspaces where wind and water erosion can redistribute resources, including sediment and seeds. Dryland restoration can incorporate methods to reduce these connected pathways, thus mitigating erosion and retaining resources locally. One method to reduce connectivity is through connectivity modifier (ConMod) structures. Quantifying sediment and seeds captured in ConMod structures provides insight into resource movement on the landscape and system-level resilience. We quantified sediment and germinable seeds captured in ConMods in relation to vegetation along a grassland-to-shrubland gradient, measured at multiple scales, in the Northern Chihuahuan desert, United States. We found (1) a significant but weak correlation between ConMod sediment and seed capture; (2) connectivity in the form of bare ground cover at the large and small scale correlated with sediment capture but not seed capture; and (3) sediment and seed capture were both influenced by previously implemented restoration treatments, though differentially. When investigating the capture of different seed functional groups and sizes, we found that grass seed capture increased with proximity to shrubs and that smaller seeds were both captured more frequently and more closely correlated to sediment capture. These findings have implications for the use of ConMods as restoration tools in shrub-encroached systems.

Key words: erosion, restoration, seed availability, seed dispersal, shrub encroachment, state transitions

Implications for Practice

- Sediment capture in ConMods increases as shrub encroachment and bare ground connectivity increase, suggesting that ConMods and similar techniques to reduce erosion are more effective at reducing erosional feedbacks in highly degraded areas.
- Mobile seed resources are present at moderate levels of shrub encroachment and bare ground connectivity, and capture of these resources may result in the recruitment of herbaceous species.
- At high levels of encroachment and bare ground connectivity, mobile seed resources are limited. Supplemental seeding may increase the success of recruitment in ConMods in highly degraded areas.
- At the patch scale, seed density is greater closer to shrubs; thus, seeding in ConMods or similar structures could be targeted to bare areas further from shrubs.

Introduction

Drylands are a major component of the Earth's land surface, making up over 40% of the total terrestrial surface area (Hoover et al. 2020). Globally, a large proportion of drylands are degraded through land use and climate change, resulting in altered vegetative structure and composition, soil properties, and hydrologic conditions, with a concomitant loss of ecosystem services (D'Odorico et al. 2013). One widespread shift in vegetation associated with dryland degradation is the encroachment of woody plants into historic perennial grasslands (Eldridge et al. 2011; Archer et al. 2017). Multiple mechanisms may increase the prevalence of woody plants in an ecosystem;

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woody plants have deep roots that can access water in deeper soil layers (which is particularly beneficial with increasing aridity) and less susceptibility to erosion driven soil losses, while herbaceous species are preferentially grazed (Berdugo et al. 2022). Advanced stages of woody plant encroachment, hereafter referred to as encroachment, can lead to a host of changes in ecosystem structure and function. For example, plant biomass becomes more heterogeneous and isolated in shrub patches, leading to increases in the size of bare plant interspaces (Huenneke et al. 2002). Functional changes in shrub-encroached grasslands can include decreased biodiversity and altered carbon dynamics, although these changes are highly context-dependent (Barger et al. 2011; Eldridge et al. 2011; Ratajczak et al. 2012).

Encroachment-driven structural and functional changes in the ecosystem amplify feedbacks, making a shrubland state self-reinforcing (Schlesinger et al. 1990). These feedbacks are closely coupled with eolian (wind-driven) and fluvial (water-driven) processes, which organize dryland vegetation patterns; large unvegetated interspaces between shrubs increase the influence of eolian and fluvial transport processes, particularly during extreme weather events (Parsons et al. 2003; Okin et al. 2006; Webb et al. 2021). This increased transport then changes the local availability of nutrients and the supply of propagules available for germination in the seed bank (Schlesinger et al. 1990; Alvarez et al. 2012). Eolian and fluvial deposition can redistribute and concentrate resources from interspaces to shrub canopies, resulting in "islands of fertility," or areas of increased nutrient cycling and water infiltration (Schlesinger et al. 1990). Together, reduced propagule and nutrient availability and ongoing erosion severely limit the ability of herbaceous plants to recruit and persist in the interspace areas (Okin et al. 2006). Further, past certain aridity thresholds, the effects of eolian erosion may exceed fluvial erosion, leading to coarser soil textures, increased infiltration of water into the soil, and further reinforcement of vegetation with deep roots (Berdugo et al. 2022).

Amplifying feedbacks at the plant-interspace scale can then translate to coarser scales. Bare plant interspaces serve as connected pathways—areas that allow free movement of wind and water through open vegetation patches. As heterogeneous shrub cover replaces more continuous grass cover, these connected pathways become longer and lead to wind erosion or sediment deposition at increasingly coarser scales, further separating deposited resources from the source (Okin et al. 2006; Webb et al. 2021). This can ultimately lead to loss of resources, including sediment, nutrients, and seeds from the system. Thus, there is an emerging framework to understand dryland dynamics that describes those landscapes with many large, bare plant interspaces as having a high degree of connectivity (Okin et al. 2015). Landscape connectivity in this context is the extent to which materials can move throughout the system and stands in contrast to the common definition of connectivity as the movement of organisms between resource patches. Bare ground connectivity and its influence on increased erosion and sediment loss have broad implications at the global scale (Okin et al. 2006; Ravi et al. 2011).

In systems that have crossed a critical threshold of encroachment, return to a grassland state is uncommon (D'Odorico et al. 2012; Peters et al. 2020; however, see Peters et al. 2012). Various restoration techniques have been implemented to reduce the movement of sediment by wind and water in bare areas (thereby altering eolian and fluvial connectivity) and, in turn, encourage the recruitment of desirable herbaceous species (Okin et al. 2015; Peters et al. 2020). There is a broad body of work on techniques to trap resources and rehabilitate degraded ecosystems, many of which were originally used by indigenous communities. Examples include the use of stone structures (Martyn et al. 2022), vertical straw "checkerboards" to stabilize sand dunes (Li et al. 2006), brush piles (Tongway & Ludwig 1996), and strategically placed fallen logs (Bowman & Facelli 2013). Building on this framework of capturing resources to restore an ecosystem, plus-shaped structures made of steel mesh placed in areas of bare ground, known as connectivity modifiers (hereafter referred to as ConMods), are being utilized for similar purposes in the southwestern United States (Rachal et al. 2015; Fig. 1). ConMods can increase perennial grass establishment and cover by capturing resources transported by wind and water as well as creating favorable microsites for germination (Fick et al. 2016; Duniway et al. 2019; Peters et al. 2020). By helping to overcome the amplifying feedbacks that limit recruitment in the plant interspace, ConMods may help revert systems that have experienced encroachment back to a grassland state (Fick et al. 2016; Peters et al. 2020).

Seed availability and dispersal are critical components of the resilience, or recovery potential, of a system after degradation occurs (Bakker et al. 1996; Török et al. 2020; Ma et al. 2021). Most seed dispersal research has been focused on primary seed dispersal, which is the period of dispersal between leaving the parent plant and finding the ground surface (Bochet 2015). However secondary dispersal, or the subsequent movement of seeds until germination or death, is more likely to affect vegetation dynamics across broader scales (Chambers & MacMahon 1994; Bochet 2015). Investigations of secondary seed dispersal by wind and water can bolster understanding of seed availability on the landscape, particularly in arid environments where wind and water transport are important (Okin et al. 2018). Ultimately, insight on seed fate can improve management and restoration efforts in degraded dryland systems by allowing us to maximize retention, and ultimately recruitment, of desirable species. Seeds, along with sediment and litter, have been reported to be moving on the landscape and captured in ConMods, thereby contributing to their effectiveness in herbaceous plant recovery (Okin et al. 2015; Fick et al. 2016; Peters et al. 2020). Quantifying the number and identity of seeds in transit will allow us to better understand the potential for ecosystem recovery and the linkages between abiotic transport vectors and biotic components of the system.

Building on past and current efforts to understand the role of connectivity in ecosystem function, particularly in shrub-encroached systems, our study investigated dryland sediment and seed capture in ConMods. More specifically, we examined how sediment and seed capture in ConMods differed in response to (1) broad and local-scale differences in connectivity along a shrub-encroachment gradient and (2) dryland restoration treatments aimed at improving grass recovery. We predicted that sediment and seed capture would both increase with connectivity along a grassland-to-shrubland gradient, due to increased transport by wind and water in those areas. We also predicted

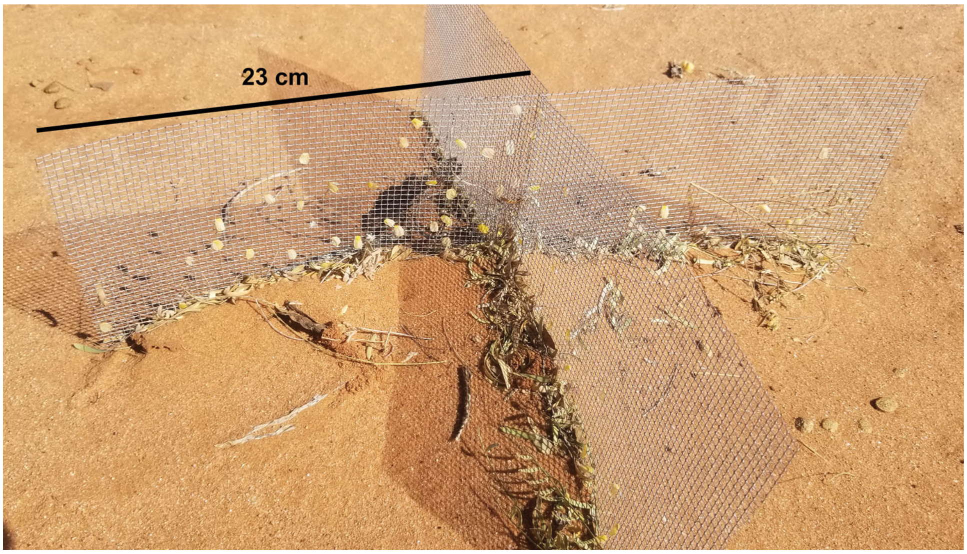

Figure 1. Representative connectivity modifier (ConMod) approximately 2 months after installation in the field, with evidence of sediment, litter, and seed collection.

that restoration treatments that reduced patch-scale connectivity would decrease sediment and seed capture compared to controls or shrub removal treatments, and this relationship would be most evident in encroached areas.

Methods

Study Area and Experimental Setup

This study was conducted at the U.S. Department of Agriculture Jornada Experimental Range (JER) in southern New Mexico (32.5°N, 106.45°W). The range is part of the Jornada Basin Long-Term Ecological Research (LTER) site, which encompasses approximately 100,000 ha of the northern Chihuahuan Desert. Mean daily temperatures range from 15 to 38°C, and mean annual precipitation at the site is 23 cm, with most precipitation falling in large, pulsed events during the summer monsoon season. Strong winds and associated sediment transport can occur during these localized convective storms. In addition to monsoon driven events, there are strong and directional spring winds which drive large sediment transport events, mostly come from the southwest (Wainwright 2006).

Our study was conducted in association with a previously established long-term research site at the JER known as the Cross Scale Interactions Study (CSIS). This site is characterized as historic black grama (*Bouteloua eriopoda*) grassland that is experiencing varying degrees of encroachment by honey mesquite (*Prosopis glandulosa*) shrubs. It is located on the basin floor, where eolian processes dominate due to ecological sites with sandy or shallow sandy soils (Peters et al. 2020; Burkett & Bestelmeyer 2023). The CSIS was established in 2013 to investigate how mechanisms across spatial scales may interact to encourage grass recovery. The CSIS consists of discrete blocks established along a shrubland-to-grassland gradient. Each of these blocks contains four restoration treatment plots: (1) herbicide treatment to kill *Prosopis glandulosa* shrubs (herbicide), (2) addition of an 8 × 8 m array of ConMods (ConMod array), (3) both herbicide treatment of *P. glandulosa* and addition of the ConMod array (herbicide + ConMod array), and (4) a control with no restoration treatments applied. We placed seed catchment plots 3 m southwest and northeast of each of the four CSIS plots (in association with each restoration treatment listed above) at eight blocks along the established gradient ($n = 64$; Fig. 2).

Field Installation and Background Data Collection

As our questions centered on seed and sediment movement, ConMods installed directly for this study served as a catchment "plot" and were sampled to assess seed and sediment capture. While they are similar in form, it is important to note the difference between our individual catchment ConMods, which we installed in 2019 to investigate seed and sediment capture, and the restoration treatments within the CSIS, which include an array of ConMods used as a patch-scale restoration tool (installed by LTER researchers in 2013). Our catchment ConMods for this study were the only ones sampled in a manner to quantify seed and sediment capture—the CSIS ConMod array was one of the restoration treatment variables used to understand the effects of restoration on seed and sediment capture.

All of our catchment ConMods were placed in areas of low vegetation cover to reduce the direct impacts of nearby vegetation on sediment and seed movement (Webb et al. 2021). ConMod construction followed a protocol similar to Fick et al. (2016) with two 15 cm × 46 cm strips of steel mesh hardware cloth arranged in a plus shape and affixed to the ground using landscape staples (Fig. 1). For consistency, all ConMods were oriented in a similar direction, with one panel parallel to and one perpendicular to the prevailing winds, which come from the southwest at approximately 240° (Wainwright 2006). We

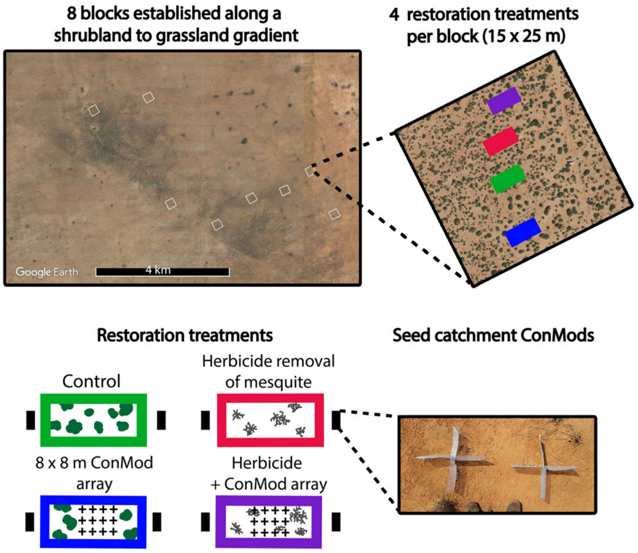

Figure 2. Experimental setup of the Cross Scale Interactions Study (CSIS) and placement of associated seed catchment plots. CSIS blocks are placed along a shrubland-to-grassland gradient and each contains four restoration treatments. Seed catchment plots associated with this study were placed southeast and northeast of each treatment. Coarse-scale bare ground values were derived from the 250 × 250 m area surrounding the CSIS block, CSIS treatments were applied at the patch-scale (10 × 15 m) and fine-scale bare ground values were taken in the 1 × 2 m area surrounding the seed catchment plots.

installed our catchment ConMods in the summer of 2019 and sampled material captured in fall 2019 to measure material moving during peak seed drop and associated dispersal.

To assess questions regarding the influence of aboveground vegetation on seed movement, we characterized vegetation at multiple scales. For the fine-scale aboveground vegetation surrounding the seed catchments, we determined species-level percent cover at the plot level by visually analyzing a 1 × 2 m area surrounding our catchment ConMods. The long axis of the plot was oriented northwest to southeast. Due to past research on the wind sheltering effects of upwind vegetation, we assessed the effect of individual nearby shrubs on sediment and seed capture by recording the distance from our catchment ConMods to the nearest shrub in the field, as well as the height and width of that shrub (Webb et al. 2021).

To characterize coarse-scale aboveground vegetation along the shrubland-to-grassland gradient, we collected unmanned aerial system (UAS) derived red, green, and blue (RGB wavelengths) imagery of a 250 m by 250 m area surrounding each of the blocks with a DJI Phantom 4 Pro with a 4K camera (Dà-Jiang Innovations, Shenzhen, China) in September 2020. Flight elevation was 60 m. Flight plan creation and image post-processing were conducted in DroneDeploy software (DroneDeploy, San Francisco, CA, U.S.A.). The resulting orthomosaic images had a resolution ranging from 1.63 to 1.75 cm/pixel.

Seed Collection and Seedling Emergence Trials

In November 2019, we removed all material captured in our seed catchment ConMods. We collected only in the direct footprint of the ConMod, which measured 0.1 m^2. To avoid sampling the belowground soil seed bank, we collected only the sediment transported to the base of the wire mesh.

After materials were collected from the ConMods, they were dried at room temperature for a minimum of 48 hours and stored in dark and dry conditions at approximately 4°C for 30 days for dry cold stratification (Baskin & Baskin 1998). We sieved the materials to 2-mm to break up soil aggregates and remove large litter, returning any removed seeds to the sample. To determine the amount of sediment collected in our ConMods during the observation period, we weighed the sample material less than 2 mm.

To quantify germinable seeds collected in our ConMods, we conducted a seedling emergence study that closely followed methods commonly used for seed banks (Gross 1990; Faist et al. 2013). To conduct the emergence study, we placed the samples in 1020 tray inserts (cells) with vermiculite as a base substrate and scaled to ensure depth in each cell to be between 0.5 and 1.5 cm. We included eight control cells to account for any contaminant species germination. Any species that grew in the control cells were removed from the analyses.

The emergence trials were conducted at the New Mexico State University, Las Cruces, United States, campus greenhouses. Temperature in the greenhouses fluctuated seasonally, ranging from 8 to 36°C. Relative humidity in the greenhouses averaged 49%. Cells were watered at least once daily and monitored for seedling emergence weekly. We transplanted representative individuals of each unique species into a potting soil mixture to allow for the growth of observable identifying characteristics. For positively identified species, information about seed size was obtained from Flora of North America (Flora of North America Editorial Committee 1993–2021), using the largest dimension reported for the seed (including any structures known to be associated with the seed through observation of the species) to separate the seeds into broad size categories: less than 3 mm = small, 3–6 mm = medium, greater than 6 mm = large. Positively identified individuals were intermittently removed to control competition effects.

Many species in dryland systems are known to produce dormant seeds (Kildisheva et al. 2019). To address this and release as many germinable seeds as possible from the samples, trials included multiple sequential treatments and a variety of techniques to break the dormancy of the seeds (Table 1). Due to the COVID–19 pandemic, the first dry down period occurred in a private residence garage; the study was moved back to the greenhouse for the second watering treatment. Cells were randomized between watering treatments to control for environmental heterogeneity in the greenhouse.

To assess if dormancy break cues were met, after the emergence trials were completed, a subset of soil samples from 8 field plots were visually sorted using a dissecting microscope to identify remaining seeds. The density of remaining seed was generally low, representing only a small portion of the seeds found in the soil samples.

Data Analyses

Bare ground cover at coarse scales correlates with landscape connectivity; thus, bare ground cover at the block scale served as our measure of connectivity over the shrubland-to-grassland gradient (Okin et al. 2015). To obtain block-scale bare ground cover values, object-oriented classification of UAS imagery was conducted in eCognition Developer 8 (Trimble Geospatial, Munich, Germany). For each image, we first ran a multiresolution segmentation algorithm, then conducted a binary classification with bare ground and vegetation classes. For each class, 30–40 representative samples were selected. The samples were used to conduct nearest-neighbor classification using the mean values of each of the three bands in the RGB imagery, brightness, and spectral difference to neighbor objects. Accuracy assessment of classified images was conducted in ArcMap 10.7.1 (ESRI, Redlands, CA, U.S.A.). A stratified random sampling scheme was used to generate 30 points, and classes were determined manually for the entire object containing each point and subsequently compared with the classification results. Total accuracy for each classified image was over 90%.

All subsequent statistical analyses were conducted using the statistical software R version 4.0.2 (R Core Team 2020). To analyze the factors that influenced sediment weight (g) captured in our ConMods, we fit a linear mixed model (package lme4; Bates et al. 2015). Percent bare ground at the block scale (250 m × 250 m), CSIS restoration treatment, catchment ConMod orientation in relation to the restoration treatment plot (southwest or northeast), percent bare ground at the local level (1 m × 2 m), distance to the nearest shrub, and size of the nearest shrub were included in the full model as fixed effects and block as the random effect. We also investigated interactions between percent bare ground at the block scale, restoration treatment, and orientation to the restoration treatment plot. Likelihood ratio tests were used for model comparison. Model assumptions were checked using the Performance package (Lüdecke et al. 2021). The r^2 values reported are marginal and conditional r^2 statistics, based on Nakagawa et al. (2017). Marginal r^2 values represent the variance explained by fixed factors, while conditional r^2 values represent the variance explained by both fixed and random factors. To meet the assumption of normality of residuals, the sediment weight data were log transformed. Correlations between sediment and seed collected were analyzed using Kendall's rank correlation coefficient.

To analyze the effect of connectivity and restoration treatments on germinable seed counts from the emergence trials, negative binomial mixed effects models were fitted with seed counts as the response variable. Total seed counts and grass seed counts were modeled. The fixed and random effects included were the same as those in the sediment models. Forb seeds were analyzed with a similar model containing only restoration treatment as a fixed effect to investigate pairwise comparisons. For all negative binomial models, Akaike information criterion (AIC) was used for model comparison, and the R package DHARMa was used to check model assumptions (Hartig 2021). Post hoc pairwise comparison tests for all models were conducted with the package emmeans (Lenth 2021).

We were interested in further investigating the relationship between the weight of sediment and the number of seeds that were collected in our ConMods. To this end, correlations between sediment and the seed collected were analyzed using Kendall's rank correlation coefficient.

Results

Our catchment ConMods accumulated an average of 290 g of sediment in their 0.1 m^2 footprint (2900 g/m^2) over the 3-month period between installation and removal of material (Table 2). The model with the best fit for the weight of sediment captured included local (1 m × 2 m) bare ground percentage, block level (250 m × 250 m) bare ground percentage, and restoration treatment (control, herbicide, ConMod array, and herbicide + ConMod array) as fixed factors. Interaction terms between percent bare ground at the block level and the restoration treatment did not improve model fit. Most of the variance in the weight of sediment captured was explained by the

Table 1. Emergence trial treatments.

Treatment	*Duration*	*Type*	*Start date*
Pre-treatment	4 weeks	Cold stratification	21 November 2019
1	9 weeks	Watering	28 January 2020
2	5 months	Dry down	30 March 2020
3	11 weeks	Soil stirring, watering	20 August 2020
4	9 weeks	Dry down	5 November 2020
5	10 weeks	Soil stirring, watering, gibberellic acid	6 January 2021

Table 2. Mean ± SE of sediment weight, total seed counts, and grass seed counts collected within the footprint of the ConMods (0.1 m^2) associated with restoration treatments in the CSIS site.

Treatment	*Sediment weight (g/m²)*	*Seeds (counts/m²)*	*Grass seeds (counts/m²)*
Control	3779 ± 372	320 ± 50	180 ± 30
Herbicide	2544 ± 381	230 ± 50	100 ± 20
ConMod array	2551 ± 296	170 ± 30	80 ± 10
Herbicide + ConMod array	2715 ± 372	290 ± 60	70 ± 20

restoration treatments and bare ground percentage at the local and block (broad) scale, with only a small amount of variance explained by the remaining unmeasured variables in the blocks (conditional $r^2 = 0.548$, marginal $r^2 = 0.461$).

We observed 1607 germinable seeds captured across 62 of our 64 catchment ConMods, representing 23 genera. This closely matches the richness found by surveying plot-scale cover across our study blocks, where we observed 26 genera. We were able to identify most individuals to the genus level (90%), with the most commonly captured being perennial grasses in the genus *Sporobolus* (28.5%), the annual forb *Nama hispidum* (22.7%), and the perennial forb *Baileya multiradiata* (8.3%). Most seeds collected (74.8%) were small seeded (<3 mm). In broad functional groups (grass, forb, subshrub, and shrub), grass seeds were collected in 59 of the 64 seed catchment plots and forb seeds were collected in 61 of the 64 plots. In contrast, shrub seeds were collected in only 19 of the 64 plots. Most grass seeds collected were perennial species (99.5%). In contrast, most forb seeds captured were annuals (80.5%).

The model that best explained the total number of seeds captured in our catchment ConMods included only restoration treatment as a fixed factor. Like the sediment weight data, interaction terms between percent bare ground at the block level and restoration treatment did not improve model fit. However, in contrast to the sediment weight model, most of the variance in the total number of seeds captured was explained by block (included as a random effect) and little by the fixed effects (conditional $r^2 = 0.642$, marginal $r^2 = 0.216$).

When modeling grass seeds captured, distance to the nearest shrub significantly improved the model, with seed capture decreasing as distance from the shrub increased ($\chi^2(1) = 9.89$, $p = 0.002$; Fig. 3). The model with best fit also included restoration treatment as a fixed factor. In the model investigating grass seeds as the response variable, fixed effects still explained a small amount of variation compared to random effects (conditional $r^2 = 0.655$, marginal $r^2 = 0.298$).

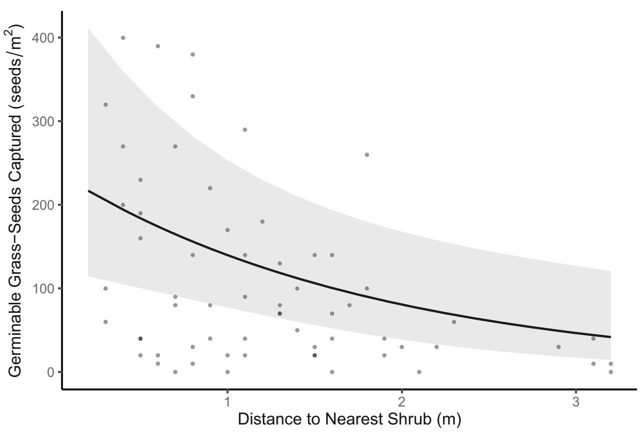

Figure 3. Effect of distance to the nearest shrub on the count of germinable grass seeds collected in ConMods at the CSIS site. Confidence band represents 95% CI.

Seed and Sediment Capture With Changing Connectivity at Multiple Scales

We were able to quantify differences in percent bare ground cover for the eight 250-m^2 blocks along the shrub-to-grassland gradient through analysis of our UAS-derived imagery. Bare ground cover within each block ranged from 55 to 74%. Sites with greater black grama cover (i.e. sites representing the reference state) tended to have a lower total bare ground percentage than sites experiencing more advanced encroachment (Fig. S1).

The sediment weight collected in our catchment ConMods was higher in blocks that contained a greater percentage of bare ground cover ($\chi^2(1) = 7.63$, $p = 0.006$; Fig. 4A). The amount of sediment collected also increased with the amount of bare ground at the local scale ($\chi^2(1) = 6.06$, $p = 0.014$). In contrast, when modeling seeds collected as a response variable, including measures of block-scale cover or local-scale cover did not improve the model (Fig. 4B).

Seed and Sediment Capture With CSIS Restoration Treatments

When addressing differences in sediment capture in our catchment ConMods associated with the CSIS restoration treatments (herbicide, ConMod array, herbicide + ConMod array, and control), post hoc tests determined that less sediment was captured in our catchment plots associated with the ConMod array restoration treatment compared to control areas with no restoration treatments ($p = 0.016$; Fig. 4A). Post hoc tests of total seed capture across the restoration treatments found significantly fewer captured seeds in the ConMod array restoration treatment areas compared to both control areas ($p = 0.001$), and the combined herbicide and ConMod array restoration treatment ($p = 0.023$). There were no other significant pairwise differences (Fig. 5A).

When breaking down seed captured by plant functional group, post hoc tests indicated that there were significantly more grass seeds captured in our ConMods associated with control plots compared to those associated with the combined herbicide and ConMod array restoration treatment ($p < 0.001$; Fig. 5B). When investigating forb seed, the patterns observed were similar to the total seeds captured, with catchment ConMods associated with the greater ConMod array restoration treatment capturing significantly fewer forb seeds than those associated with the control treatment areas ($p = 0.048$) and the combined herbicide and ConMod array restoration treatment ($p < 0.001$; Fig. 5C). There was no evidence for an interaction between connectivity measures and the CSIS restoration treatments for any of the variables observed.

Correlations Between Sediment and Seed Capture

Though we did not see a mirrored relationship between sediment and seed capture over the shrub-encroachment gradient, based on Kendall's rank correlation coefficient, there was a significant positive correlation between the sediment weight captured and the total amount of seeds captured ($\tau = 0.38$, $p < 0.001$; Fig. 6). We found that small seeds were more strongly correlated with sediment weight than medium or large seeds ($r_\tau = 0.49$, $p \leq 0.001$, Fig. 7).

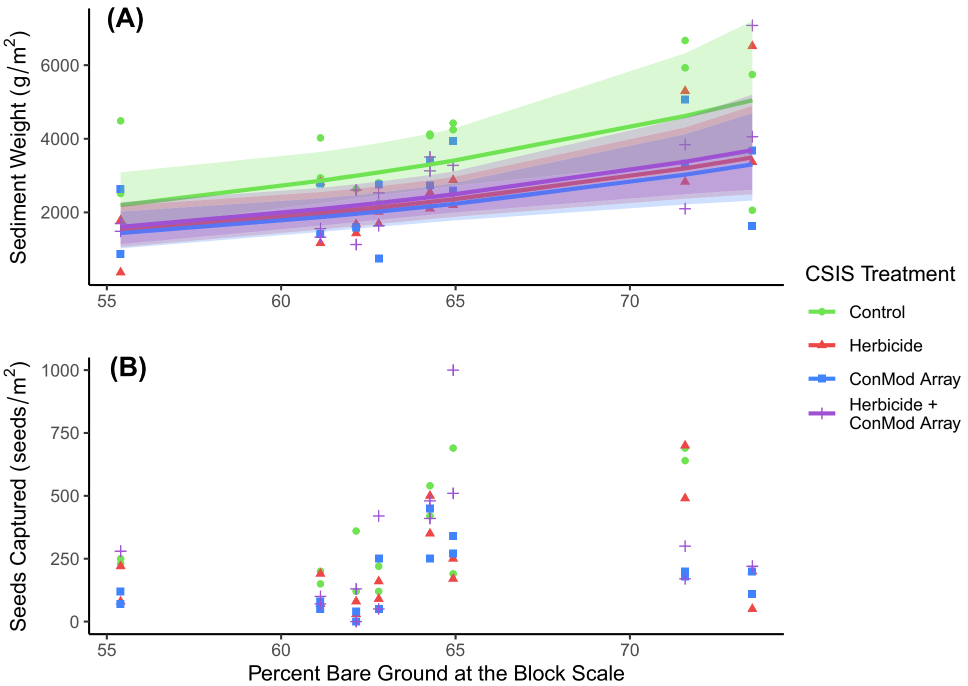

Figure 4. Effects of bare ground percentage at the block (250 × 250 m) scale and Cross Scale Interactions Study (CSIS) treatments on (A) the weight of sediment captured and (B) the total number of germinable seeds captured in seed catchment ConMods. Confidence bands represent 95% CI.

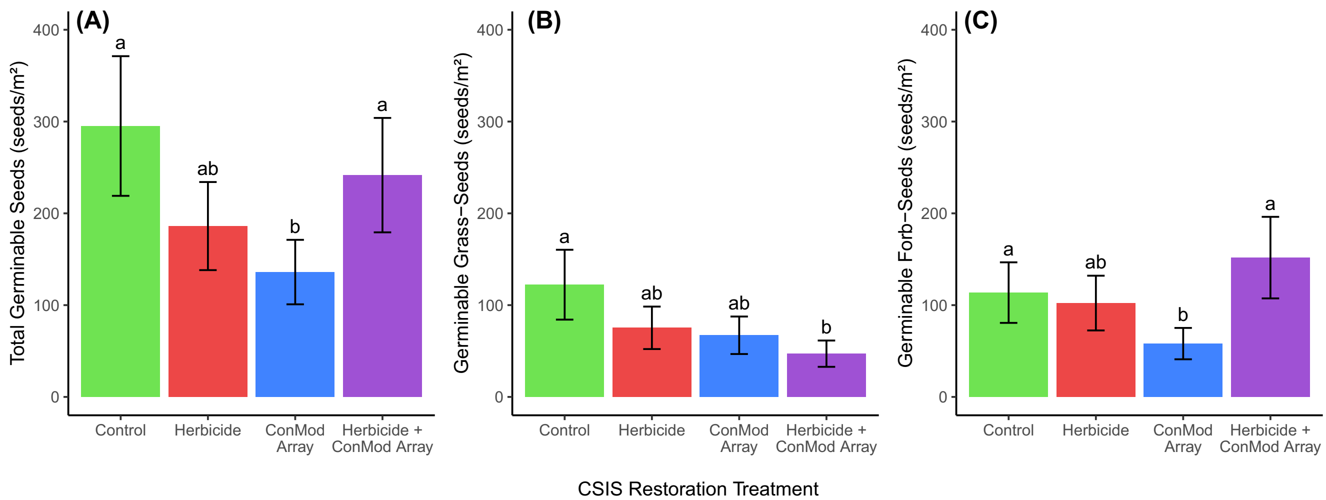

Figure 5. Estimated marginal means of counts of (A) total germinable seeds, (B) germinable grass seeds, and (C) germinable forb seeds captured within the footprint of seed catchment ConMods, grouped by association with Cross Scale Interaction Study restoration treatments. Shrubs and subshrubs made up a negligible portion of all seeds collected and so are not shown as individual functional groups. Error bars represent ±1 SE.

Discussion

Seed dispersal has important implications for the recovery potential of ecosystems and is especially pertinent in dryland systems that are highly influenced by wind and water transport (Aguiar & Sala 1997; Okin et al. 2018). Our investigation of captured materials across a shrub-to-grassland gradient helped determine how connectivity, as measured by bare ground cover at various scales, is affecting sediment and seed movement. In general, we found that germinable seeds were moving at high rates on the landscape, including a high proportion of small-seeded, herbaceous species of interest for restoration. Many of the captured germinable seeds were perennial grass species, which shows an inherent recovery potential for these species if they can be retained. We hypothesized that there would be a strong relationship between the total amount of seeds and sediment captured along this gradient. We found that this correlation was not very strong, and evidence that there are additional variables affecting the total number of seeds captured. However, small seed capture had a stronger correlation with sediment capture and small-seeded species appear to be moving longer distances in secondary seed dispersal.

In line with our prediction of increased connectivity resulting in increased sediment movement, we found that our ConMods captured more sediment as connectivity, as measured by bare ground cover, increased at both the local and block scale. This finding aligns with research that shows higher rates of eolian sediment flux and hydrologic connectivity in more disturbed, shrub-dominated sites compared to more continuously vegetated grassland sites (Gillette & Pitchford 2004; Li et al. 2006; Turnbull & Wainwright 2019; Webb et al. 2021). This also suggests that ConMods and similar structures are more effective in decreasing abiotic erosional feedbacks in more degraded areas. Tongway and Ludwig (1996) similarly found appropriately placed brush piles were more effective at capturing material in areas experiencing grazing disturbance. In contrast, we did not find a predictable relationship between seed capture and our connectivity measures at either scale—instead, we discovered there may be a threshold of vegetation cover where seed transport drops but sediment transport increases.

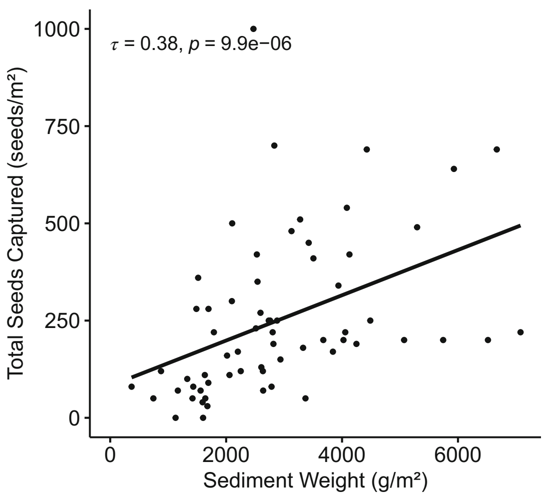

Figure 6. Kendall rank correlation between the weight of sediment and counts of germinable seeds captured in ConMods as determined by germination trials. Kendall τ coefficient and p value are reported.

In areas with low bare ground cover at the block scale, sediment capture was low, and we hypothesize that vegetation structure is also constraining seed movement. Conversely, the low numbers of seed in transit in the blocks with higher bare ground cover, despite high levels of sediment transport, suggest a lack of available seed sources in these areas. In the Colorado Plateau, a cooler desert than our study, *Sporobolus* seeds were added to ConMod arrays, leading to increased recruitment of *Sporobolus* seedlings (Fick et al. 2016). This, coupled with our findings, indicates seed limitation is a constraint for plant recruitment in ConMods in areas with high connectivity. Peters et al. (2020) found variable recruitment in ConMods in the Chihuahuan desert despite no addition of seeds; areas with low recruitment were also attributed to low seed availability. Our study suggests that these recruitment patterns are due to heterogeneous seed capture in ConMods, even in sites with shared soil and geomorphic traits. It is likely that investigating herbaceous cover or seed production (i.e, of seed-producing grasses), specifically at an intermediate scale, would give insight into seed availability and further illuminate thresholds of cover that constrain seed capture.

There are numerous factors that could lead to low seed availability, beyond the low cover of seed-producing grasses. It is likely a portion of the seeds captured were seeds from past growing seasons that remained dormant in the soil seed bank and were subsequently transported during our study. This is supported by our finding that small-seeded species capture correlates with sediment capture and previous research which shows species with persistent seed banks tend to be small (Thompson 1987). In this case, a depleted seed bank could contribute to patterns of low seed capture in degraded areas. Alvarez et al. (2012) demonstrated that the seed bank can be quickly depleted following vegetation removal. Additionally, depletion of seed could be due to

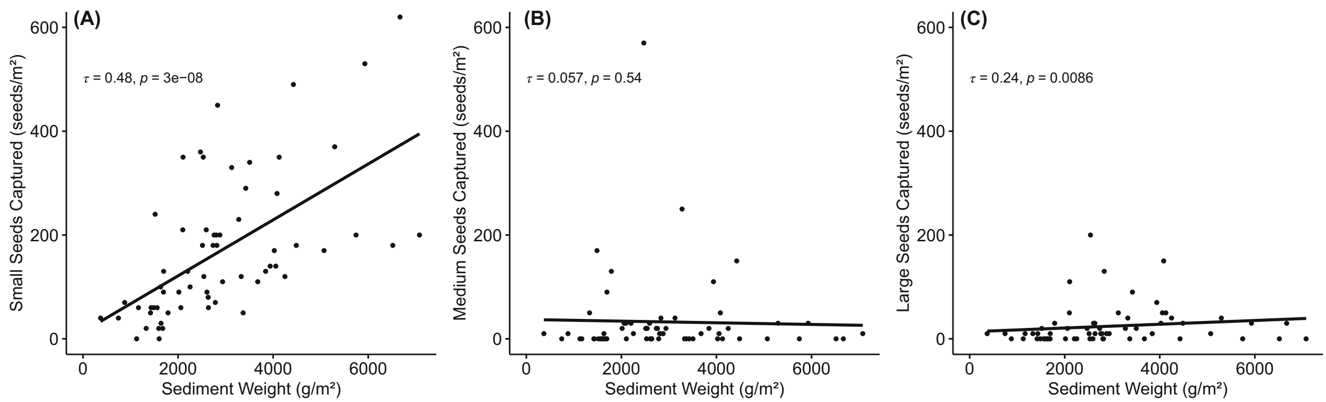

Figure 7. Kendall rank correlation between the weight of sediment and counts of germinable seeds captured in seed catchment ConMods, grouped by seed sizes: (A) small (<3 mm), (B) medium (3–6 mm), and (C) large (>6 mm). Kendall τ coefficient and p value are reported.

increased seed predation pressure in the more shrub-encroached areas (Reichman 1979; Kerley et al. 1997).

Along with a lack of available seed, the lack of a relationship between vegetation cover and seed capture could be due to a mismatch in the scales of seed movement and our measures of bare ground cover, or connectivity. Our methods of measuring seed capture do not allow us to determine whether seed movement and homogenization of seed resources may be occurring at larger scales and overriding differences in seed capture that we measured, or at even smaller scales than those measured. The total distance at which seeds move from the parent plant to germination merits further investigation.

Both sediment and seed capture did have a significant relationship with the previously implemented CSIS restoration treatments. Contrary to our prediction that CSIS patch-scale restoration treatments (herbicide use, ConMod arrays, or a combination of herbicide and ConMod arrays) would be more effective in reducing transport of materials in more degraded areas, there was no evidence for an interaction between restoration treatments and coarse-scale cover on either sediment or seed capture. This indicates that the effects of the restoration treatments on seed and sediment capture were similar along the observed grassland-to-shrubland gradient at the time measured. In terms of sediment, this could be in part because we measured the materials captured in our catchment ConMods during the monsoon season. Rachal et al. (2015) found that net sediment flux, measured with Big Spring Number Eight dust samplers, differed in areas with reduced connectivity (via a ConMod array) compared to control areas only during the spring windy season but not the fall monsoon season.

Two opposing effects of the CSIS restoration treatments could lead to the patterns of seed capture we observed. First, increased seed retention within the patch could be due to decreased connectivity (i.e. capture in the ConMod array), as evidenced by the fewer seeds we captured in our plots associated with the ConMod array restoration treatment compared to controls. Conversely, any vegetative recruitment responses to the CSIS restoration treatments could increase seed availability, and therefore capture in our seed catchment ConMods—this could be one reason why no differences were observed between the control and combined herbicide and ConMod array restoration treatments. The divergent responses observed by forb and grass seeds may also be a result of vegetative recruitment in the restoration plots as individual species may have had different responses to the implemented restoration treatments. Future effort placed on relating the plant community response to the CSIS treatments, including measures of fecundity, to seed movement in adjacent areas could help illuminate the seed dynamics uncovered in this study.

One interesting biological result, at the patch scale, was the relationship between grass seed capture and proximity to nearby shrubs. Across a few-meter gradient, ConMods placed closer to shrubs captured more grass seeds, which is consistent with research that shows shrubs acting as reservoirs of grass seed, but also suggests that these resources are not static (Reichman 1984; Caballero et al. 2008). Mesquite shrubs can also act as nurse-plants, promoting recruitment and the establishment of seedlings via the "islands of fertility" concept (Schlesinger et al. 1990).

As connectivity increases, so does movement and the capture of sediment. Seeds, however, are subject to a myriad of variables, and increases in connectivity may eventually lead to a lack of seed availability that becomes decoupled from increased movement of material. Restoration treatments which capture mobile resources, such as ConMods, are promising tools to reduce connectivity and capture mobile sediment and viable seeds in dryland systems. Nearly all ConMods sampled in this study contained seeds (62 of 64 total). If successful germination occurs in these structures, they work to alter the amplifying feedback of erosion in shrubland interspaces and shift the system back from a shrubland to a grassland state. More investigation into the factors that affect seed availability, movement, and recruitment on the landscape will help to better utilize ConMods as restoration tools.

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Supporting Information

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

Figure S1. Representative UAS-derived imagery and resulting image classification from three blocks along the shrubland-to-grassland gradient.

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