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# Modifying connectivity to promote state change reversal: the importance of geomorphic context and plant–soil feedbacks

Debra P. C. Peters,[1,2,6] Gregory S. Okin,[2,3] Jeffrey E. Herrick,[1,2] Heather M. Savoy,[1,2]
John P. Anderson,[2,4] Stacey L. P. Scroggs,[2,5] and Junzhe Zhang[2,3]

[1] *U.S. Department of Agriculture, Agricultural Research Service, Jornada Experimental Range Unit, Las Cruces, New Mexico 88003 USA*
[2] *Jornada Basin Long Term Ecological Research Program, New Mexico State University, Las Cruces, New Mexico 88003 USA*
[3] *Department of Geography, University of California, Los Angeles, California 90095 USA*
[4] *Jornada Experimental Range Department, New Mexico State University, Las Cruces, New Mexico 88003 USA*
[5] *Department of Biology, New Mexico State University, Las Cruces, New Mexico 88003 USA*

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*Abstract.* Alternative states maintained by feedbacks are notoriously difficult, if not impossible, to reverse. Although positive interactions that modify soil conditions may have the greatest potential to alter self-reinforcing feedbacks, the conditions leading to these state change reversals have not been resolved. In a 9-yr study, we modified horizontal connectivity of resources by wind or water on different geomorphic surfaces in an attempt to alter plant–soil feedbacks and shift woody-plant-dominated states back toward perennial grass dominance. Modifying connectivity resulted in an increase in litter cover regardless of the vector of transport (wind, water) followed by an increase in perennial grass cover 2 yr later. Modifying connectivity was most effective on sandy soils where wind is the dominant vector, and least effective on gravelly soils on stable surfaces with low sediment movement by water. We found that grass cover was related to precipitation in the first 5 yr of our study, and plant–soil feedbacks developed following 6 yr of modified connectivity to overwhelm effects of precipitation on sandy, wind-blown soils. These feedbacks persisted through time under variable annual rainfall. On alluvial soils, either plant–soil feedbacks developed after 7 yr that were not persistent (active soils) or did not develop (stable soils). This novel approach has application to drylands globally where desertified lands have suffered losses in ecosystem services, and to other ecosystems where connectivity-mediated feedbacks modified at fine scales can be expected to impact plant recovery and state change reversals at larger scales, in particular for wind-impacted sites.

*Key words: aeolian processes; alternative states; cusp-catastrophe model; desertification; ecohydrology; long-term studies; regime shifts; remediation.*

## INTRODUCTION

Many ecosystems are susceptible to environmental shocks that result in changes in structural and functional properties leading to alternative states (IPCC 2014, Rocha et al. 2015). The persistence of these states is closely linked with hysteresis, in which processes and drivers governing the transition from one state to another are different from the ones governing the transition back to the original state (Scheffer et al. 2001). Feedbacks that maintain the properties of a new state through time can make transitions back to a former state challenging under current biotic, edaphic, and climatic conditions (Schlesinger et al. 1990, Kéfi et al. 2016). As a result, few studies have documented successful reversals (e.g., Suding et al. 2004, Herrick et al. 2006, Peters et al. 2012), and recent research has focused on identifying early warning indicators or the conditions that could signal a shift prior to a state change to allow early intervention (Bestelmeyer et al. 2011, Clements and Ozgul 2018). Because many ecosystems have already crossed thresholds leading to changes in state with subsequent changes in ecosystem services (Rocha et al. 2015), there is a critical need to understand the underlying processes governing feedbacks, yet this understanding alone is often insufficient to promote state change reversals (Suding et al. 2004). Positive interactions that modify soil conditions may have the greatest potential to alter self-reinforcing feedbacks under certain conditions (Kéfi et al. 2016). The challenge for any given ecosystem is to understand the underlying mechanisms and their relationship

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[6] E-mail: deb.peters@usda.gov

with environmental conditions (climate, soils) that may provide opportunities for state change reversals (Peters et al. 2012). Our goal was to modify connectivity of resources by wind or water on different geomorphic surfaces in an attempt to alter positive plant–soil feedbacks and shift woody plant-dominated states in drylands back toward perennial grasses. Drylands exemplify alternative stable states where perennial grasslands have converted to dominance by xerophytic, unpalatable, woody plants in arid and semiarid ecosystems globally (Archer 1989, Westoby et al. 1989, Schlesinger et al. 1990).

Drylands cover ~40% of the Earth's land surface (MEA 2005) and impact ~2 billion people (Reynolds and Stafford Smith 2002). Thus, persistent state changes have consequences for vital ecosystem services, such as air and water quality as well as food production at local to global scales (Peters et al., 2014). Many dryland systems have been studied to examine the hysteretic dynamics that cause multiple stable states (e.g., Rietkerk et al. 2004, Kéfi et al. 2007). In landscapes that experience woody plant encroachment into perennial grasslands, land use, climate, and perhaps other exogenous factors, create conditions favorable to establishment and dominance by woody plants, and unfavorable to recruitment and survival by perennial grasses (Archer 1995, Okin et al. 2009, D'Odorico et al. 2010). Drought and livestock overgrazing can disrupt plant-scale feedbacks that re-enforce woody-plant-dominated states by reducing grass cover and allowing woody plant recruitment and growth to occur through competitive displacement of grasses by shrubs (Archer 1995). Through time, a threshold is crossed when the dominant processes change and another set of feedbacks emerges such that woody plants dominate, namely, the patch-scale redistribution and transport of water, soil resources, and propagules within and out of low-grass, woody-plant-dominated patches (Schlesinger et al. 1990, Li et al. 2007). As the area dominated by woody plants increases, another threshold can be crossed where land–atmosphere interactions dominate to overwhelm these plant- and patch-scale processes (Peters et al. 2004, Beltrán-Przekurat et al. 2008).

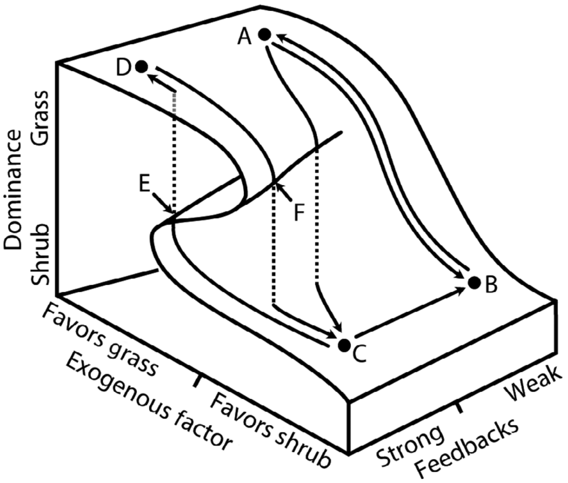

FIG. 1. Cusp-catastrophe theoretical diagram. Transitions from a stable grassland to a feedback-stabilized woody plant-dominated system can occur if the strength of feedbacks changes (A → C), such as when increasing bare gap size increases connectivity-related feedbacks caused by wind and water erosion. A woody-plant-dominated state (point B), can be reversed if the exogenous factors change to favor grass recovery (B → A). A woody-plant-dominated system stabilized by feedbacks (point C) may revert to a perennial grassland (panel a, point D), but the exogenous forces be much more favorable for a woody-plant-to-grassland transition (C → E→D) than they were for the grassland-to-woody plant transition (panel a, D → F→C). Because states are enforced by feedbacks, moving a system into the equilibrium regime potentially entails the suppression of positive feedbacks that stabilizes the woody-plant-dominated state (C → B→A).

Viewed from the perspective of cusp-catastrophe theory, a grass-woody system is "in equilibrium" when dominance by woody plants or by perennial grasses is governed by exogenous factors. In an equilibrium grassland (Fig. 1, point A), factors that lead to loss in grass cover and a switch to woody-plant-dominated states (Fig. 1, point B, A → B) can be reversed to once again favor grasses if the exogenous factors change to favor grass recovery (Fig. 1, B → A). However, strong feedbacks lead to alternative stable states, and systems exhibiting this behavior are often termed "disequilibrium" (Turnbull et al. 2012). A woody-plant-dominated system that is stabilized by feedbacks (Fig. 1, point C) may revert to a perennial grassland (Fig. 1, point D), but the hysteresis inherent in these systems requires that the exogenous forces be much more favorable for the woody-plant-to-grassland transition (Fig. 1C → E → D) than they were for the grassland-to-woody-plant transition (Fig. 1, D → F→C). Transitions from a stable grassland to a feedback-stabilized woody-plant-dominated system can also occur if the strength of feedbacks changes during this transition (Fig. 1, A → C), such as when increasing bare gap size increases connectivity-related feedbacks caused by wind and water erosion (Okin et al. 2009). The grassland-to-woody-plant-dominated transition has been reported all over the world and often exhibits a critical characteristic of non-equilibrium systems: rapid, seemingly irreversible transitions in response to exogenous forcing (e.g., Bestelmeyer et al. 2015).

In the early considerations of disequilibrium systems, the feedbacks were invoked mainly at the plant-interspace scale where a reduction of grass cover leads to the movement of soil resources by wind or water from bare interspaces between plants to microsites under woody plant canopies (e.g., Schlesinger et al. 1990). This concentration of resources continues to enforce the poor performance of grasses and good performance of woody plants within a landscape mosaic. More recently, the horizontal movement of resources along connected pathways occurs that serve as important components of feedbacks (Fig. 1, A → C) at larger spatial scales between sources and sinks across a landscape (e.g., Ludwig et al. 2005). This transport allows loss of nutrients and water from woody-plant-dominated systems as a whole, as well as more efficient redistribution within these systems, with the effects on grasses being stronger than the effects on shrubs, leading to enforcement of woody-plant-dominated states. The idea of "connectivity" has thus become an important concept in understanding the emergence and resilience of alternative stable states (Okin et al. 2009, Stewart et al. 2014).

However, in the American Southwest where these transitions have been well documented, paleo-data associated with large-scale changes in climate indicate that woody-plant-dominated conditions have reverted to grasslands several times in the past 10,000 yr (Buck and Monger 1999). Until recently, it was not clear what kind of climatic conditions might favor return of grasses in disequilibrium systems (Fig. 1,C → D). Peters et al. (2014) reported that several consecutive years with above-average precipitation increases seed availability and stolon/tiller density such that grasses can respond effectively to rain in subsequent years. These results strongly indicate that, through a series of wet years (>4 yr), grass production can be restored in such a way that the hysteresis of the grass–woody system can be overcome and grasses can once again become important components of the system (Fig. 1, C → D→E). This grass recovery in degraded shrublands requires either long-term change of the climate toward conditions favoring high plant available water or a sequence of wet years favoring grass establishment and persistence. The probability of these events in the future is unknown, although increases in multi-year extreme events are one possible scenario in the American Southwest as a consequence of global warming (Cook et al. 2015, Jones and Gutzler 2016).

The cusp-catastrophe model thus suggests an additional route for the reemergence of grasses as landscape dominants, namely moving the system into the equilibrium regime (Fig. 1, C → B). Once in that regime, the system may return to a grass-dominated state in equilibrium with climate without the need for an exceptional sequence of wet years (Fig. 1, B → A). Because states are enforced by feedbacks, moving a system into the equilibrium regime potentially entails the suppression of feedbacks that stabilizes the woody-plant-dominated state. Given the hypothesized importance of lateral transport by wind and water in stabilizing these feedbacks by woody plants coupled with the role of bare gap connectivity in permitting this transport (Okin et al. 2009), this analysis can be tested. Thus, we hypothesized that grasses can be reestablished and persist through time, even during average weather conditions, if bare gap connectivity between woody plants can be reduced.

Research using short-lived isotopes has shown that reducing bare gap connectivity through the addition of small structures (connectivity modifiers, ConMods) decreases lateral transport, thus reducing the flow and increasing the deposition of sediment (Rachal et al. 2015). Through time, we expect this accumulation of material will include litter and propagules as well as sediment. Localized reductions in bare soil evaporation combined with additions of herbaceous seeds lead to germination and short-term (2 yr) establishment of grasses and forbs in these islands of fertility (Fick et al. 2016). However, it is unknown under what conditions modifying connectivity can alter plant–soil feedbacks for perennial grass persistence through time under variable rainfall, and if successful grass recovery depends on geomorphic context where water or wind is the dominant vector of transport.

Here we report the results of an experiment in which we reduced bare ground connectivity on three geomorphic surfaces with different relative importance of transport by wind or water at a research site in the northern Chihuahuan Desert, the Jornada Basin USDA-LTER site. We developed and installed "connectivity modifiers" (ConMods) in an effort to modify plant–soil feedbacks and reestablish perennial grasses in bare gaps between woody-plant-dominated vegetation. Short-term (2 yr) success of ConMods with addition of seeds and soil disturbance was shown by Fick et al. (2016) using the methods we developed for the experiment reported here. Our objectives were twofold. First, we sought to determine how grass recovery is modified by geomorphic context by comparing long-term (9 yr) plant growth and litter accumulation for three locations. We hypothesized that grass recovery would occur following litter accumulation regardless of the vector of transport because bare soil evaporation should decrease and available water to grass seedlings should increase *only* after litter amount increases in bare soil interspaces between shrubs. Second, we sought to examine the relative importance of plant–soil feedbacks vs. precipitation to grass recovery through time. We hypothesized that grass cover would be related to precipitation amount in the first few years of the experiment, and to precipitation and sediment accumulation in the latter years of the study. Plant–soil feedbacks were expected to become important through time as islands of fertility grow and develop under grass canopies, similar to positive feedbacks under shrub canopies in the desertification process (Schlesinger et al. 1990). As grass canopies increase in size, nutrients, propagules, and water would be trapped beneath their canopies; thus leading to positive feedbacks to grass growth.

## METHODS

### *Study area*

The study was conducted at the USDA Jornada Basin Long Term Ecological Research (JRN) site in southern New Mexico, USA (32.5° N, 106.45° W). Climate is arid to semiarid with an average of 24 cm/yr precipitation (80-yr average), occurring mostly (>60%) during the summer to fall monsoon period (1 July to 1 October). Average monthly temperatures over the same time period ranged from 6°C in January to 26°C in June. Livestock grazing has generally decreased over time (Fredrickson et al. 1998). Current grazing intensities are maintained at low levels (<500 domestic grazers on average) throughout the 100,000-ha site.

To test the effectiveness of ConMods for modifying transport by wind or water, we selected three locations on soil-geomorphic units with different transport potential by wind or water. All three locations were perennial grasslands in the 1850s that converted to shrublands between 1900 and 1950 (Gibbens et al. 2005). The “aeolian” location was selected to represent level alluvial plains of the basin floor sand sheet (“ap[w]” in Monger et al. 2006) where surface soils are loamy sands with negligible slope (<1%). The dominant broad-scale transport vector is wind, although local water redistribution can occur under high intensity rainfall events (Peters et al. 2009). Vegetation is dominated by honey mesquite (*Prosopis glandulosa*) with subdominant perennial grasses, including black grama (*Bouteloua eriopoda*) and dropseeds (*Sporobolus* spp.), at low densities (Drewa and Havstad 2001). The other two locations represent different landform units on the piedmont slope (bajada) where water is the dominant transport vector (Monger et al. 2006). These locations occur on silty and gravelly soils. Vegetation is dominated by creosotebush (*Larrea tridentata*) with perennial grasses such as black grama and bush muhly (*Muhlenbergia porteri*) at low densities (Havstad et al. 1999). The “alluvial-active” location is on an alluvial fan collar on a geomorphically active alluvial fan piedmont surface (“fp” in Monger et al. 2006) at an average slope of 2.08%. The “alluvial-stable” location occurs on a geomorphically stable alluvial fan remnant (“af” in Monger et al. 2006) at an average slope of 3.06%.

### *Design and fabrication of ConMods*

ConMods were fabricated from two 20 cm tall × 50 cm wide panels of 0.64 cm mesh galvanized hardware cloth (Fig. 2a). Each panel had a 10-cm slit at the midpoint along its long side, such that two panels could fit together in a “+” shape. Each ConMod was attached to a 50 cm long × 0.64 cm diameter steel rod at each of its four ends. An additional rod was attached to the slit where the panels crossed to provide structural integrity. Each ConMod was anchored by inserting these five rods vertically into the ground to a depth of 15 cm. This placement at the ground surface was expected to trap material (soil, litter, seeds, water from overland flow) within the ConMod structure, as well as to decrease bare soil evaporation and increase water available to seeds trapped within each ConMod at the plant scale. Control structures consisted only of the five vertical rods without the hardware cloth (Fig. 2a).

### *Experimental design*

In April–July 2008, eight replicate 8 × 24 m plots were established and fenced from livestock at each location (aeolian, alluvial-active, alluvial-stable). Paired treatment and control plots were located on similar soils, topographic relief, and percent cover of vegetation; the treatment plot was randomly assigned. Each plot consisted of three contiguous ~8 × 8 m patches: an upwind/upslope patch, a center patch (ConMod manipulation or control), and a downwind/downslope patch. In each center patch, a 1 × 1 m grid was temporarily installed, either aligned with the direction of the prevailing winds (aeolian) or perpendicular to the slope (alluvial). A ConMod was placed in the center of each 1 × 1 m grid cell that did not contain perennial plants (Fig. 2b). This cell size was selected to reduce the connected pathways for wind (i.e., distance between existing perennial plants and future plants based on ConMod locations) to <1 m. At this diameter, aeolian sediment movement that could damage seedlings through abrasion is minimized. Similarly, water movement is slowed by smaller gaps, thus increasing infiltration (Okin et al. 2006). Because the patch area and the number of initial perennial plants were variable for each plot, the number of ConMods installed in each treatment patch varied (19–52). The same procedure was followed for control patches, but only steel rods were installed to simulate soil disturbance of the rods.

### *Vegetation response and material accumulation*

From 2008–2016, we monitored response within a subset of individual ConMods or control structures (35.4 × 35.4 cm = 0.125 $m^2$; Fig. 2a) using digital photos at a resolution of 12.1 MegaPixels with image dimensions of 4,000 × 3,000 pixels. Only a subset of points within each patch was monitored because of the time-consuming nature of photo interpretation. Vegetation and litter cover were estimated from overhead photos, and the vertical accumulations of litter and soil material were measured from lateral photos. The same 10 ConMods or control structures (initially randomly selected) per center patch were photographed at least once a year (except 2011 was excluded). Standardized overhead photos were obtained from ~85 cm height aboveground with the camera positioned horizontally above the center rod. Lateral photos were taken to include the full width of each ConMod at least once a year in 2008, 2012, 2015, and 2016 at ground level from each cardinal direction. For each overhead photo, a 10 × 10 grid of points was manually classified into one of seven groups: forb, grass, shrub, subshrub, seedling, litter, or bare soil using SamplePoint 1.5 (Booth et al. 2006). The total number of points in each group was tabulated for each photo, and then divided by the total for all groups to obtain the percentage of points occupied by each group. The percentage

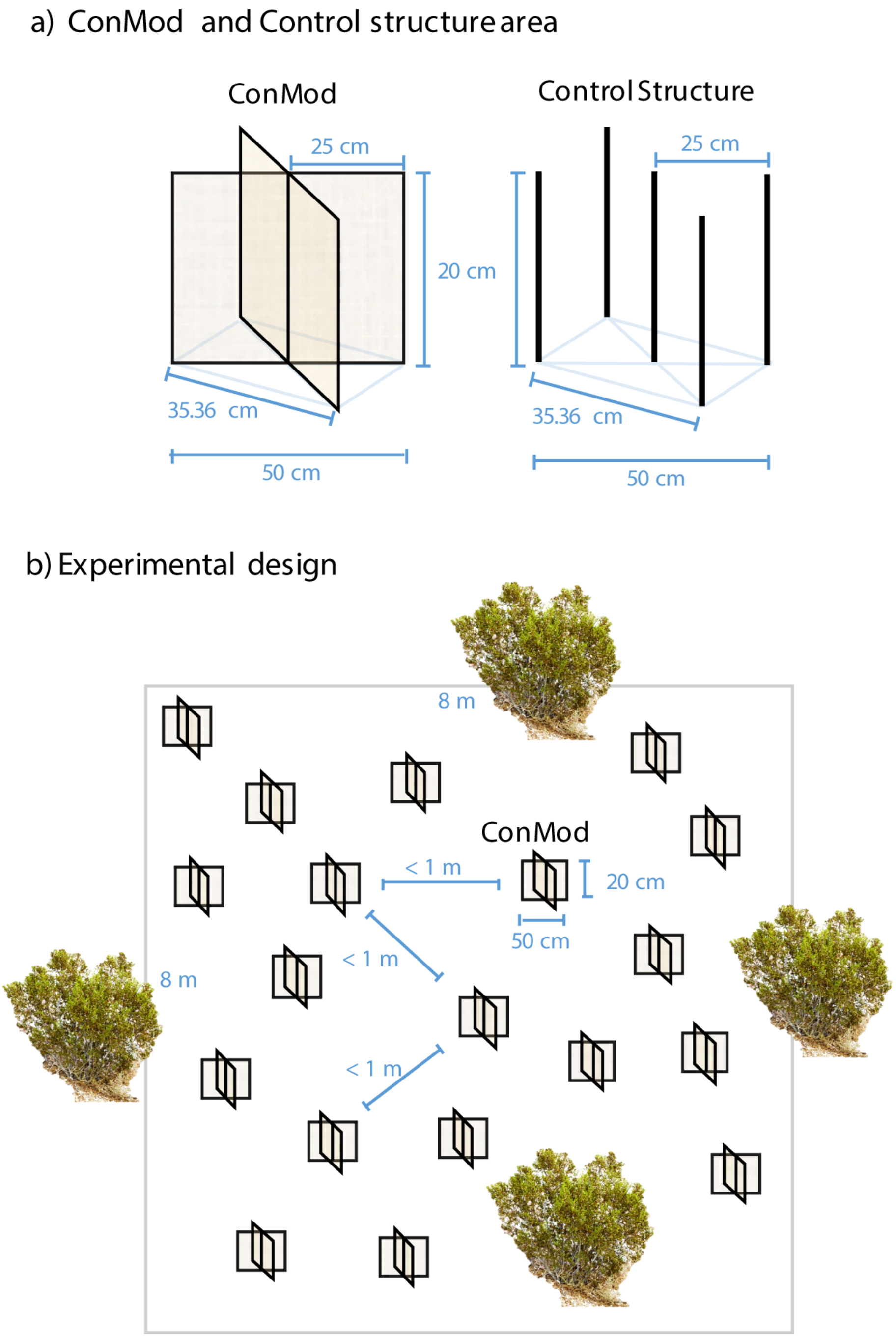

FIG. 2. Conceptual diagram of modifying connectivity to overcome patch-scale resource redistribution by wind or water. (a) Area defined by ConMod or control structure. (b) Experimental design showing individual ConMods (50 cm wide × 20 cm tall) spatially distributed within an ~8 × 8 m treatment patch at 50–100 cm distance apart.

cover of herbaceous plants (i.e., forbs and grasses) and litter were calculated at the plant scale (ConMod) for each patch for each sampling year.

For each lateral photo, we measured the distance from six predetermined points evenly spaced along the top of the ConMod mesh to the litter and to the soil surface in each quadrant of the ConMod (SigmaScan Pro 5.0; Systat Software, Inc., San Jose, CA USA) using Trace Measurement Mode with Distance measurement option. Due to vertical movement of mesh over time, adjustments in calculations were performed to correct for shifting reference points. The distance difference between years for the same points was a measure of the change in vertical accumulation of litter or soil. The average and standard error change in vertical accumulation for litter or soil since 2008 at the scale of a plant (ConMod) across a patch were calculated for each sampling year and location.

We used imagery obtained from an unmanned aerial vehicle (UAV) in 2017 to count the number of plants in all ConMods or control structures within each patch. Because ConMods and control structures were established in micro-locations where there were no plants in 2008, plants detected in the 2017 imagery were recruits after the study began. A Phantom 4 UAV with a 4K camera was flown over each patch in July during a single day between 11:00 and 13:00. The Phantom 4 was flown at 6–10 m height to obtain the highest possible resolution. Overlap and sidelap were 60% in these images. Structure-from-motion (SfM) software (Metashape; Agisoft LLC, St. Petersburg, Russia) was used to align the imagery and create a dense 3D point cloud from which an orthophoto was constructed with 8–10 mm resolution. At this resolution, individual grasses, forbs, or shrubs can be distinguished, though they cannot be identified to the species level. Plants in ConMods or control structures were visually classified as either grass, forb, or shrub on each image.

### *Environmental variables*

Monthly precipitation (cm) was obtained from the nearest weather station within 1–2 km for each location and summed to total precipitation from the six-month period preceding observations in each year. Long-term precipitation (1915—2019) obtained from the USDA ARS headquarters was used for context (24 cm/yr). The aeolian location had the lowest average precipitation (21.9 cm) compared with the other two locations (24.8 alluvial-active; 25.0 cm/yr alluvial-stable; Fig. 3). For most years, all three locations had similar dry years (2009, 2011, 2012), wet years (2008, 2015), and average years (2010, 2013, 2014). Year types were defined based on amounts relative to the three location means obtained during the duration of this study and the long-term mean (1915–2019; Fig. 3). Wet years had rainfall amounts larger than all four mean values, dry years had rainfall amounts less than all four mean values, and average years had rainfall amounts similar to the four mean values in each year. The locations diverged in 2016 where one location was wet (alluvial-stable), one was average (alluvial-active), and one was dry (aeolian).

Two stems of windborne sediment collectors located 2 m apart in the upwind and downwind adjoining areas of each patch were installed in 2008 at each location. Each stem consisted of two Big Springs Number Eight (BSNE; Custom Products and Consulting, Big Spring, Texas, USA) collectors mounted at two heights (10 and 30 cm). This distance between stems and heights of collectors were based on long-term collections from the Jornada using this method (Gillette and Pitchford 2004). Collectors were oriented at 240° azimuth corresponding to the dominant wind direction during the spring windy season (Li et al. 2007). Material from each collector was obtained approximately quarterly through mid-2011, and once a year in May or June from 2012 to 2016. Sediment transport for each BSNE (g·cm$^{-2}$·d$^{-1}$) was calculated by dividing the dry mass per collector by opening area (10 cm$^2$) and the time interval between measurements. To obtain yearly estimates, measurements made between each May or June sampling were combined by summing dry weights and time intervals. The two collection heights were treated separately. The difference between average amount of sediment in the pair of upwind collectors and the average amount in the pair of downwind collectors for the same patch was used as an indication of erosion or deposition within a patch (see Rachal et al. 2015). A greater amount of sediment leaving a patch than entering a patch (negative difference) is an indication of net erosion; conversely, more sediment entering a patch than leaving (positive difference) is an indication of net deposition. To control for variable sediment entering a plot, relative net sediment fluxes were calculated by dividing net sediment fluxes by incoming sediment flux.

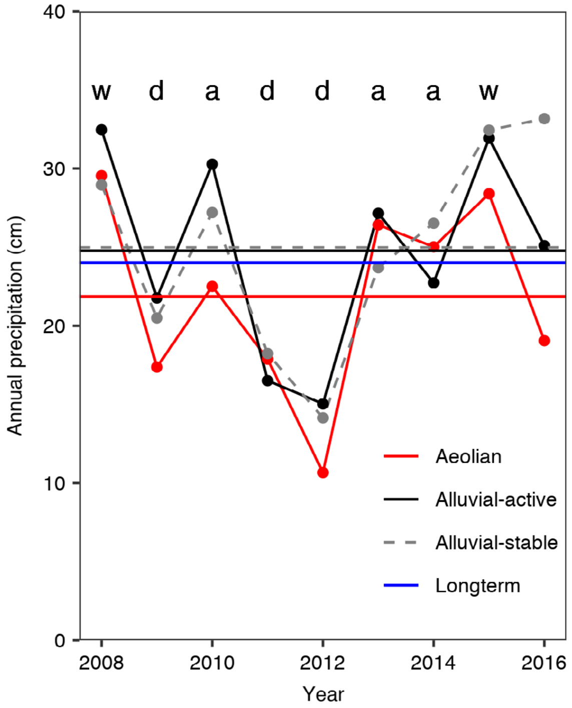

FIG. 3. Precipitation through time at each of three locations. Annual precipitation (cm) from nearby weather station in three locations: aeolian, alluvial-active, and alluvial-stable. Horizontal lines indicate location means over the study period, and the long-term mean (1915–2019) from the USDA ARS headquarters. w = wet year; a = average year; d = dry year.

### *Statistical analyses*

Repeated measures analysis of variance was performed for plant-scale vegetation and litter cover, and sediment flux separately for each location in the R statistical environment (v3.5.1; R Core Team 2018). For plant-scale vegetation and litter cover, treatment and year were fixed factors, and annual percentage cover measurements at each patch were repeated measures. Student *t* tests were used to compare plant-scale vegetation and litter cover among locations. For UAV imagery, a Pearson's chi-squared test was conducted for each location and plant type. For plant-scale sediment and litter accumulation in ConMods, standard errors of the mean vertical accumulations for each sampling year relative to 2008 were calculated to compare the variability in accumulation over time and between locations. For sediment flux, treatment and year were fixed factors and annual relative net sediment flux measurements at each patch were repeated measures. A significance level of 0.05 was used for all analyses.

## RESULTS

### *Objective 1: Geomorphic context and plant recovery*

In support of our first hypothesis, experimentally modifying connectivity resulted first in an increase in litter cover regardless of the vector of transport (wind, water) followed by an increase in perennial grass cover two years later. At all three locations, litter cover increased immediately following the placement of ConMods (Fall, 2008) with significant interactions between treatment and time (Fig. 4a). Litter cover (2008–2016) at the aeolian (25.2% ± 1.8%) and alluvial-active (27.85% ± 2.2%) locations was significantly greater than litter at the alluvial-stable location (12.4% ± 0.9%). Recovery of herbaceous plants had a time lag compared to litter; significant recovery did not occur until 2014 on the aeolian and alluvial-active locations, and the interaction of treatment and time was significant for both locations. Similar to litter, herbaceous cover at the aeolian (17.3% ± 3.3%) and alluvial-active locations (16.7% ± 4.0%) from 2014 to 2016 was significantly greater than herbaceous cover at the alluvial-stable location (0.11 ± 0.02%); in addition, this location had limited herbaceous cover with no difference between ConMods and control structures (Fig. 4a). Most recovered plants after 2012 (>50%) were grasses except in the alluvial-stable location where recovery was negligible (Fig. 4a top insert).

The majority of vertical accumulation was from soil rather than litter beginning in 2012 at all three locations with lower amounts at the alluvial-stable compared with the other two locations in each year (Fig. 4b). The alluvial-active location experienced the most soil accumulation with increases over time (~15 mm in 2012 to 31 mm in 2016). The aeolian and alluvial-stable locations had soil accumulations in the range of 13–21 mm and 9–11 mm, respectively, without obvious temporal trends. Litter accumulation was minor and sometimes exhibited a net loss after 2008.

Based on UAV imagery, the proportions of plant types varied by location (Fig. 5). At the aeolian and alluvial-active locations, patches with ConMods had significantly greater proportions with grass recruits compared to controls. At the alluvial-stable location, there was a greater proportion with shrub recruits compared with controls (Fig. 5b).

### *Objective 2: Disentangling the importance of positive feedbacks and precipitation to grass recovery*

The study began in the wettest of the nine study years (2008) when nearly 80% of annual rainfall fell during the summer, yet grass cover on control plots showed only a modest response to rainfall at the aeolian and alluvial-active locations, and no response at the alluvial-stable location (Fig. 6). However, the addition of ConMods at the aeolian location resulted in grass cover being related to precipitation in the first 3 yr of our study until 2010, and then a significantly different relationship between grass cover and precipitation for the years from 2012 to 2016 (Fig. 6a). This relationship suggests that plant–soil feedbacks developed following 5 yr of modified connectivity that were maintained through time under variable precipitation with a significantly greater intercept compared to the relationship for control plots (intercept $P = 0.014$; slope $P = 0.32$). The addition of ConMods at the alluvial-active location led to grass cover values showing evidence of plant–soil feedbacks in 2014–2015 that returned to control values in 2016 with average rainfall (Fig. 3). Grasses did not respond to precipitation or ConMod structures in the alluvial-stable location (Fig. 6a).

Including net sediment flux, an indicator of patch-scale redistribution of resources, provided greater explanatory power (higher $R^2$) compared with precipitation alone for the aeolian and alluvial-active locations (Fig. 6b). At the aeolian location, plant–soil feedbacks occurred in 2013 that were maintained through 2016 whereas only 2014 and 2015 showed evidence of plant–soil feedbacks on the alluvial-active location. Combining precipitation and sediment flux together provides partial support for our second hypothesis where grass cover was related to precipitation in the first 5 yr of our study, and plant–soil feedbacks developed following 6 yr of modified connectivity to overwhelm effects of precipitation on sandy, wind-blown soils. These feedbacks persisted through time under variable annual rainfall. On water-driven soils, either feedbacks developed after 7 yr that were not persistent (active soils) or these feedbacks did not develop (stable soils).

## DISCUSSION

Alternative states maintained by feedbacks are notoriously difficult, if not impossible, to reverse. In a 9-yr study, we modified horizontal connectivity of resources by wind or water on different geomorphic surfaces in an

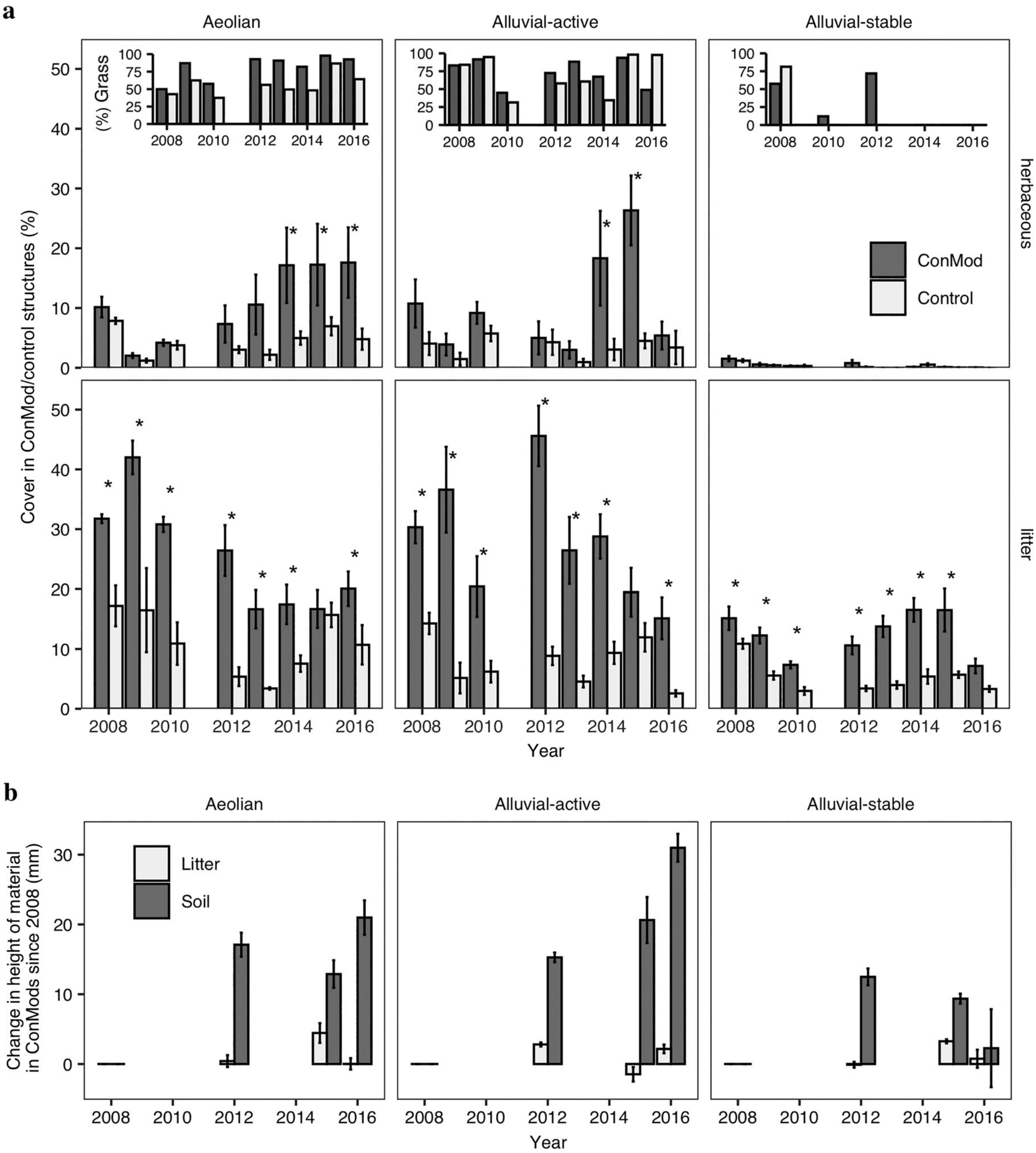

FIG. 4. Vegetation response and material accumulation through time at each of three locations. (a) Mean herbaceous and litter cover (percentage of area) from overhead imagery from 2008-2016 with inserts indicating the percentage of herbaceous cover that is perennial grass and (b) mean vertical accumulation (mm) of soil and litter since 2008 from lateral imagery in 2012, 2015, and 2016. All means are from $n = 4$ plots per treatment. Error bars denote standard error. Asterisks denote significant differences between the treatment means at $P < 0.05$.

attempt to alter plant–soil feedbacks and shift woody plant- dominated states back toward perennial grass dominance. Modifying connectivity resulted in an increase in litter cover regardless of the vector of transport (wind, water) followed by an increase in perennial grass cover two years later. Modifying connectivity was most effective on sandy soils where wind is the dominate vector, and least effective on gravelly soils on stable surfaces with low sediment movement by water. Grass cover was related to precipitation in the first 5 yr of our study, and plant–soil feedbacks developed following 6 yr of modified connectivity to overwhelm effects of precipitation on sandy, wind-blown soils. These feedbacks persisted through time under variable annual rainfall. On

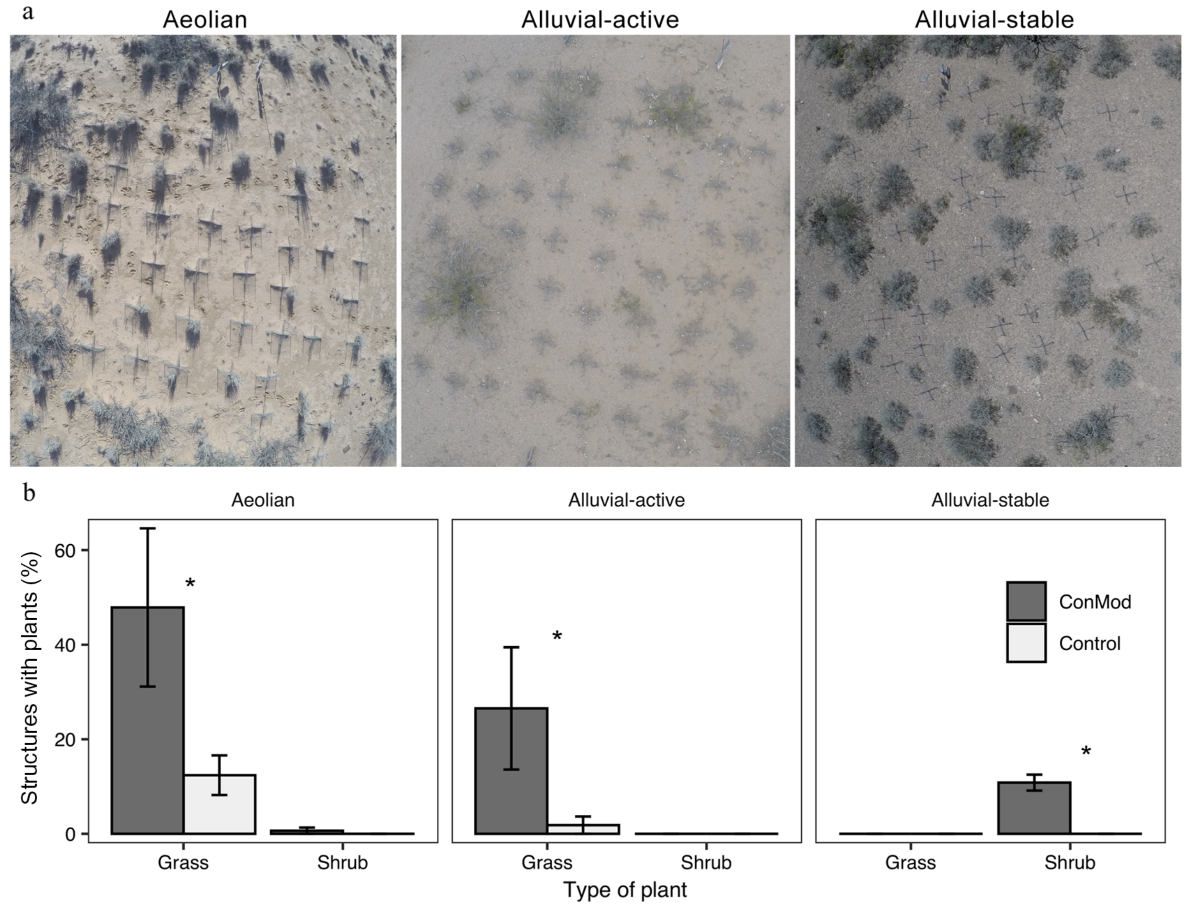

FIG. 5. New recruits in ConMod/control structures at each of three locations. (a) Example unmanned aerial vehicle (UAV) imagery from Summer 2017 over one patch with ConMods from each location, and (b) the mean proportion (%) of ConMod/control structures with new plants (grass or shrub) within the total number of ConMod/control structures per treatment ($n$ = 4). Error bars denote standard error. Asterisks denote significant differences between the treatment means at $P < 0.05$.

alluvial soils, either plant–soil feedbacks developed after 7 yr were not persistent (active soils) or did not develop (stable soils). This novel approach has application to drylands globally, and to other ecosystems where connectivity-mediated feedbacks modified at fine scales can be expected to impact plant recovery and state change reversals at larger scales, in particular for wind-impacted sites.

### *Modifying connectivity for grass recovery*

Many studies on alternative states or regime shifts in the past decade have focused on identifying characteristics of systems prior to a state change as part of an early warning strategy (Carpenter and Brock 2006, Bestelmeyer et al. 2011). However, for systems such as drylands, these state changes have already occurred over the past several centuries to result in desertification, the broad-scale conversion of perennial grasslands to dominance by woody plants (Reynolds and Stafford Smith 2002). These shifts in dominant life form are accompanied by changes in ecosystem services at the landscape scale, including loss of soil, nutrients, and water as well as changes in biodiversity and forage production (Barger et al. 2011, Eldridge et al. 2011, Peters et al. 2013). At finer spatial scales, increases in woody plant dominance lead to changes in the redistribution of soil resources within and among individual plants or patches of vegetation compared to grasslands where soil resources are more homogeneous between plants and small bare soil interspaces (<50 cm diameter; Schlesinger et al.,1990, 1995). When large shrubs or small trees encroach into grasslands, the bare soil interspaces increase in size, and erosional processes connect bare soil interspaces resulting in deposition beneath plant canopies and positive feedbacks to woody plant persistence that make it very difficult for grasses to return (Archer 1989, Schlesinger and Pilmanis 1998, Herrick et al. 2006, Okin et al. 2009).

In the current experiment, small structures (ConMods) modified connectivity with respect to wind and water movement and created adequate microsites for the establishment of grass seeds and subsequent recovery of

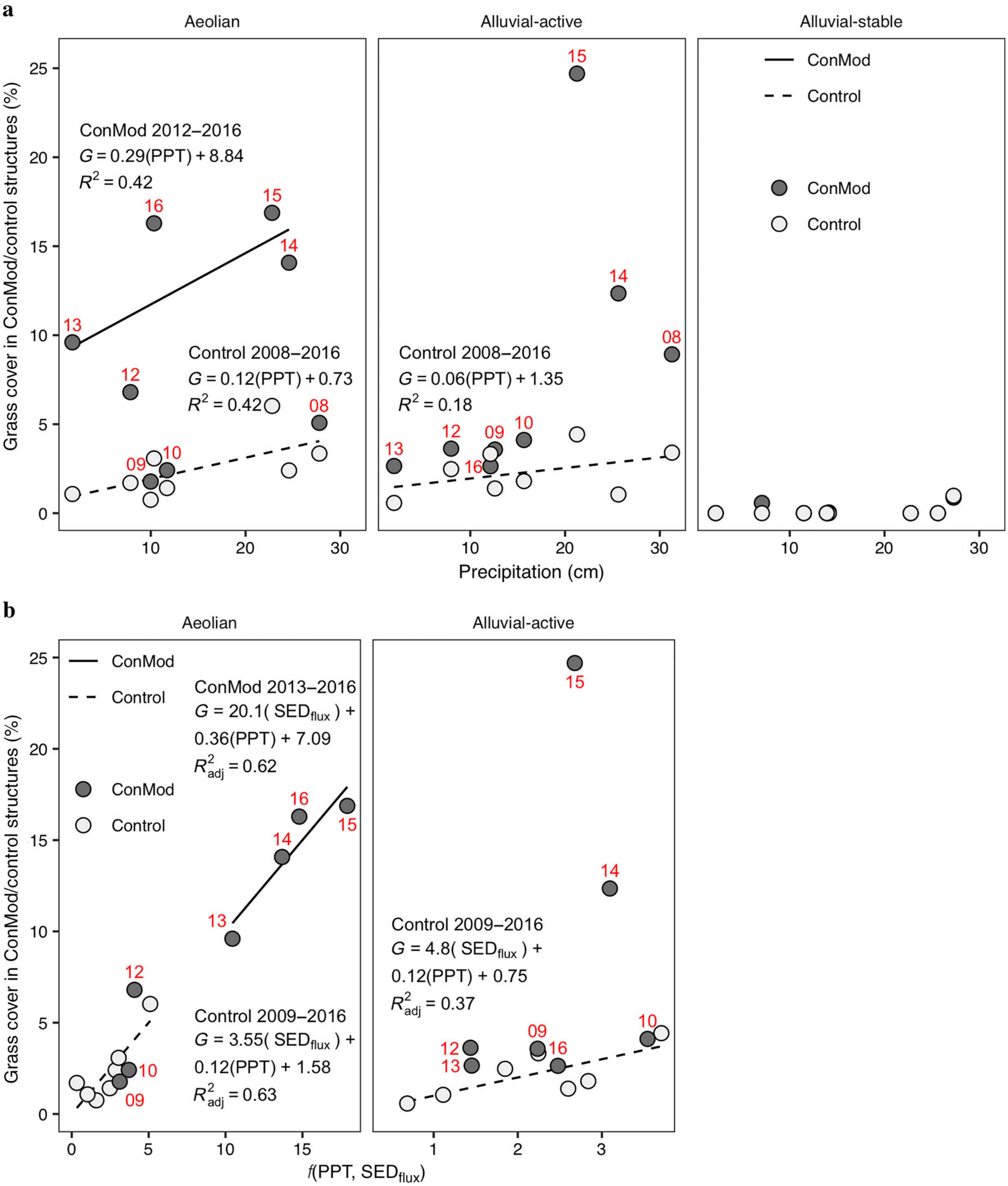

FIG. 6. Grass cover as a function of multi-scale drivers. (a) Percentage of cover attributed to grasses in ConMods as a function of precipitation (cm) in the previous six months from nearby weather station and (b) percentage of cover attributed to grasses in ConMods as a function of precipitation (PPT, cm) in the previous six months and relative net sediment flux ($\text{SED}_{\text{flux}}$, $\text{g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$). Linear regression models per treatment and location are indicated. Only significant regression models shown ($P < 0.05$). Years are indicated in red for the ConMod values at the aeolian and alluvial-active locations.

grass plants. ConMods are designed to disrupt the connectivity that re-enforces positive feedbacks maintaining shrub dominance, thus reducing ecosystem "leakiness" (sensu Ludwig et al. 2002). In the context of the cusp-catastrophe model presented earlier (Fig. 1), weakening of these connectivity-mediated feedbacks appears to move the system from the folded, disequilibrium portion of the curve (Fig. 1, points C, E, D, and F) toward the continuous, equilibrium portion of the curve (Fig. 1, points A and B). Specifically, in the shrub-dominated systems where this experiment was conducted, ConMods were expected to weaken the feedbacks associated with leakiness (Fig. 1, C → B) so that when adequate soil moisture for recruitment is available, the system can move toward a grass-dominated state. The complete return of a grass-dominated state would still require a disturbance event to result in mortality of shrubs that can live hundreds of years. In the controls without ConMods, by contrast, the shrub-dominated state with bare soil interspaces was entirely preserved even during periods of high rainfall and adequate soil moisture availability (Fig. 3) because conditions that inhibit grass recruitment, such as wind and water transport that removes seeds and litter from interspaces, could not be overcome. Thus, grass-favoring exogenous factors such as enhanced soil moisture during wet periods, were not sufficient to move the feedback-enforced shrub-dominated state (Fig. 1, point C) past the threshold (Fig. 1, point E) where grass recruitment could occur.

### *Ecogeomorphic context and strategies for remediation*

Geomorphic context is important for local soil water availability as well as the redistribution of soil and nutrients by wind and water (Monger and Bestelmeyer 2006, Duniway et al. 2018). Locations for treatments reported here were selected to be either dominated by aeolian or fluvial modes of transport of material, and fluvial locations were expected to be on stable or active surfaces (Monger et al. 2006). Our results indicate grass recruitment occurred on both the aeolian and alluvial-active locations, but that only shrub recruitment occurred on the alluvial-stable location. Our results indicate that ConMods are capable of interrupting transport, thus promoting the capture of both grass and shrub seeds in microsites where they can germinate and seedlings can become established. Because all three locations trapped sediment, the failure of grasses to establish at the alluvial-stable location may be attributed to low perennial grass seed availability at this location as shown by slow grass recovery (Havstad et al. 1999). In addition, ConMods may encourage establishment of less desirable species if those seeds are available, such as the establishment of shrubs on the alluvial-stable surface. If the goals are remediation, then addition of seeds of desirable species may be combined with ConMod treatments to ensure the establishment and recovery of perennial grasses (Fick et al. 2016).

### *Developing plant–soil feedbacks over time*

Our results suggest that localized plant–soil feedbacks within ConMod structures became more important than rainfall amount following 6 yr (aeolian) or 7 yr (alluvial-active) of modified connectivity. These feedbacks only persisted through time on the aeolian location. However, this 9-yr experiment is effectively short on ecological timespans for long-lived (>20-yr) perennial grasses. Because ConMods were able to promote perennial grass recovery over this relatively short time span, their effectiveness has been demonstrated. But, questions remain. For instance, it is not clear what the long-term consequences of ConMods are for the development of soil and for rebuilding soil carbon and nitrogen stocks. Further, our experiments do not indicate what might happen if ConMods are removed. Grass plants are expected to effectively serve as their own connectivity modifiers, and the interruption of aeolian and fluvial transport should become self-sustaining even after ConMods are removed. The amount of vegetation required for effective connectivity modification is not yet clear, and will likely depend on a number of factors, such as the dominant mode of transport (aeolian or fluvial), the soil erodibility and water holding capacity, the slope, and soil infiltration rate and capacity. Climate and weather will affect the threshold of cover required for plant-sustained connectivity modification that promotes perennial grass recovery. A period of drought will reduce the cover and number of grass plants, whereas several sequential wet years will likely promote new recruitment (Peters et al. 2014). Extreme weather events such as high winds and intense rain may cause enough erosion to reduce plant cover, whereas low winds and gentle rains may promote local-scale redistribution, water infiltration, and enhancement of the effectiveness of microsites for grass recruitment and recovery (Wainwright et al. 2002, Turnbull et al. 2013).

## CONCLUSIONS

We expand existing theory of alternative states by showing that self-reinforcing feedbacks can be disrupted by modifying connectivity of resources with impacts on resource redistribution, propagule availability, and plant growth as critical processes for a state change reversal. Our results show that time lags need to be accounted for in the development of feedbacks required for recovery. The persistence of these feedbacks depends on geomorphic surfaces that differ in transport vectors, surface soil properties, and seed availability. Our conclusions have significant implications for targeting restoration projects to maximize both short- and long-term returns on investment in ecosystems where state change reversals under current climate were previously believed to be impossible (Herrick et al. 2006, 2019).

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## DATA AVAILABILITY

Data are available from the Environmental Data Initiative, with sediment collected in BSNEs at https://doi.org/10.6073/pasta/70b2d6321f6769acb3f1a712d75650a0 and lateral photos at https://doi.org/10.6073/pasta/19667054c6810c94a49ca4c04a276e80.