ARTICLE

Special Feature: Dynamic Deserts

Mechanisms and drivers of alternative shrubland states

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Abstract

Grassland-to-shrubland state change has been widespread in arid lands globally. Long-term records at the Jornada Basin USDA-LTER site in the North American Chihuahuan Desert document the time series of transition from grassland dominance in the 1850s to shrubland dominance in the 1990s. This broadscale change ostensibly resulted from livestock overgrazing in conjunction with periodic drought and represents the classic "grassland-to-shrubland" regime shift. However, finer-scale observations reveal a more nuanced view of this state change that includes transitions from dominance by one shrub functional type to another (e.g., based on leaf habit [evergreen vs. deciduous], N_2 fixation potential, and drought tolerance). We analyzed the Jornada Basin historic vegetation data using a fine-scale grid and classified the dominant vegetation in the resulting 890 cells on each of four dates (1858, 1915, 1928, and 1998). This analysis allowed us to quantify on contrasting soil geomorphic units the rate and spatial distribution of: (1) state change from grasslands to shrublands across the Jornada Basin, (2) transitions between shrub functional groups, and (3) transitions from shrub-to-grass dominance. Results from our spatially explicit, decadal timescale perspective show that: (1) shrubland ecosystems developing on former grasslands were spatially and temporally more dynamic than has been generally presumed, (2) in some locations, shrublands initially developing on grasslands subsequently transitioned to ecosystems dominated by a different shrub functional type, with these changes in shrub composition likely involving changes in soil properties, and (3) some shrub-dominated locations have reverted to grass dominance. Accordingly, traditional, broad characterizations of "grassland-to-shrubland" state change may be too simplistic. An accounting of these complexities and transitions from one shrub functional group to another is important for projecting state change consequences for ecosystem processes. Understanding the mechanisms, drivers, and influence of interactions between patterns and processes on transitions between shrub states defined by woody plant functional types will be germane to predicting future landscape change.

INTRODUCTION

The concepts of alternative states and regime shifts in arid and semiarid ecosystems (hereafter "drylands") arose out of recognition that traditional conceptual models based on gradual, predictable plant succession could not describe the abrupt and discontinuous vegetation change that often characterizes dryland ecosystems (Lauenroth & Laycock, 1989; Westoby et al., 1989). These dynamics, now recognized as "state changes," are often maintained by strong positive feedbacks between plants and soil properties (Peters & Havstad, 2006; Ratajczak et al., 2014; Rietkerk et al., 2004). Such transitions are expected to become more common with changes in climate and disturbance regimes (Allen et al., 2009; Kelly & Goulden, 2008; Scheffer et al., 2012). Analyses of long-term data have been instrumental in characterizing and predicting state changes at small spatial scales where local processes dominate (Bestelmeyer, Brown, et al., 2011a). However, at landscape scales where heterogeneity in soils, landforms, and land management is extensive and varies within or along geomorphic- and watershed-scale gradients (e.g., elevation), the dominant process may vary through space and time to make predictions challenging (Bestelmeyer, Goolsby, & Archer, 2011b; Peters et al., 2004, 2006). Historic state changes documented using long-term data can be used to improve understanding of the spatial processes driving changes between alternative states, the positive feedbacks that maintain them, and the climatic and land management drivers that push these states into new future states (Peters et al., 2006).

Studies characterizing regime shifts in drylands have typically focused on the displacement of herbaceous vegetation states (e.g., perennial grasslands) by xerophytic, unpalatable shrub-dominated states (Archer, 1989; Schlesinger et al., 1990). Such transitions are relatively well documented and are commonly regarded as desertification in drylands (Archer et al., 2017). However, little is known about the dynamics of the shrublands known to have displaced grasslands. Current paradigms for these shrublands in the Chihuahuan Desert are based on observations over the past century and reflect interactions among recurring drought, changing land use priorities, and policy and market forces promoting overgrazing and soil erosion (Peters et al., 2015). The major shrub species proliferating in the Chihuahuan Desert grasslands were

associated with distinct topographic positions and soil types (Wondzell et al., 1996). Long-term data suggest these relatively new shrubland states are dynamic at the scale of landscape units, and may subsequently transition to alternative shrubland states (Buffington & Herbel, 1965; Gibbens et al., 2005) dominated by woody plants that differ with respect to key functional traits (e.g., stature, canopy and root architecture, leaf size, shape, texture, seasonal habit, and phenology).

Shrubland ecosystem state changes

Dryland landscapes are mosaics of grassland and shrubland ecosystem types dominated by different species and functional groups whose dynamics are influenced by the major drivers of change over the past several centuries: precipitation and livestock overgrazing interacting with topographic relief in space and temperature in time (Havstad et al., 2006). These ecosystem types occur on contrasting, often intermingled, soil geomorphic units (GMUs) where soil properties and the redistribution of resources and propagules by water or wind vary (McAuliffe, 1994; Monger et al., 2006; Rachal et al., 2012). Accordingly, robust predictions of spatial and temporal transitions have proven challenging (Bagchi et al., 2012). Although shrublands have generally increased in spatial extent at the expense of grasslands throughout the southwestern USA (Buffington & Herbel, 1965; Grover & Musick, 1990; McClaran, 2003; Yanoff & Muldavin, 2008; York & Dick-Peddie, 1969), not all shrub species and the functional groups they represent have responded to climate and grazing in a similar fashion (Archer et al., 2017). For example, the three shrub species that have displaced grasslands on contrasting soil geomorphic landscapes in the Chihuahuan Desert represent markedly different functional groups (Table 1): *Prosopis glandulosa* (honey mesquite: long-lived, winter deciduous, and drought-avoider with the potential for symbiotic N_2 fixation) on sandy soils of alluvial plains, *Larrea tridentata* (creosote bush: evergreen, true xerophyte) on coarse–loamy, skeletal soils of upper bajadas (fan piedmont), and *Flourensia cernua* (tarbush: short-lived, deciduous, and drought-tolerant) on loamy soils of lower bajadas (alluvial flats) (Figure 1; Duniway et al., 2018; Grover & Musick, 1990; Muller, 1940; Wondzell et al., 1996).

Shrubs representing different functional groups have displaced grasslands on distinctly different soil GMUs in

TABLE 1 Prominent shrubs in the Chihuahuan Desert Jornada Basin, their functional traits, and life history attributes

Attribute	Prosopis glandulosa (honey mesquite)	Larrea tridentata (creosote bush)	Flourensia cernua (tarbush)
Leaf habit	Deciduous	Evergreen	Tardily deciduous
N_2 fixation	Yes	No	No
Root system[a]	Shallow lateral and deep tap	Shallow lateral and deep tap	Shallow lateral and deep tap
Water use	Avoids drought	True xerophyte	Drought tolerant
Dispersal	Ungulates, rodents	Tumbling, rodents	Gravity, water
Livestock dispersal?	Yes	No	No
Vegetative regeneration	Yes	Yes, but uncommon in the Jornada Basin	Weak
Response to lagomorph exclusion	++	+	+
Insect enemies	Twig girdlers, bruchid beetles	−	++ (folivores, episodic)
Longevity	Centuries	Centuries	Decades
Long-lived seed bank?	Yes	No (?)	No
Soil O_2 (flooding) sensitivity	Moderate	High	Moderate
Seedling sensitivity to grass competition	Low	Unknown	Unknown

Note: Throughout the article, these shrubs are referred to as PRGL (*Prosopis glandulosa*), LATR (*Larrea tridentata*), and FLCE (*Flourensia cernua*).
[a]Gibbens and Lenz (2001).

the Chihuahuan Desert. Accordingly, the current paradigm assumes the present-day shrub species dominance patterns are dictated by the topoedaphic context (McAuliffe, 1994; Wondzell et al., 1996). However, early surveyor records and subsequent inventories in the northern Chihuahuan Desert suggest a more complicated scenario, wherein grasslands associated with long, gentle piedmont slopes extending from the base of mountain fronts to the basin floor (hereafter "bajadas") were initially displaced by tarbush, which was then subsequently displaced by creosote bush in some areas, but not others (Gibbens et al., 2005). Similarly, mesquite shrubs have typically invaded grasslands located on the basin floor characterized by sandy surface soils with a variable depth to a caliche layer (Browning et al., 2012; Peters et al., 2006) and portions of bajadas where sands had been deposited (hereafter "bajada sand sheet"). Such observations point to how little is known about how changes in surface soil properties and topography have governed the rate, pattern, sequence, and persistence of shrub species/functional group proliferation in grasslands. Such information will be necessary to project the future species/functional group composition of shrublands developing on former grasslands or shrublands of different types.

The state change concept implies that shrublands developing on former grasslands will be persistent. However, the species composition of those shrublands could potentially change with time, either toward another shrub type or toward perennial grasses. Although perennial grass recovery in shrublands has been studied (Peters et al., 2012), shifts in shrub dominance have not been examined. If shifts in shrub dominance occur, and if the new shrub species represent different functional groups, then primary production, biogeochemical cycling, hydrology, and land surface–atmosphere interactions would also change (Beltran-Przekurat et al., 2008; Felton et al., 2021; Peters et al., 2012). The narrow "grassland-to-shrubland" focus of current desertification paradigm stops short of addressing this issue. As a first step in assessing potential shrub–shrub transitions, we explored a suite of state change scenarios on contrasting soil GMUs in the Jornada Basin: the lower and upper reaches of bajadas, the basin floor, and the bajada sand sheets (Figure 1; Monger et al., 2006).

Shrubland₁–shrubland₂ transition scenarios

We developed three scenarios of landscape change in the Chihuahuan Desert and sought to ascertain which of those scenarios might lead to present-day patterns of shrub distribution. Each scenario presumes initial (1850s) dominance by perennial grasses (Peters et al., 2012) and subsequent declines in their cover (Peters et al., 2015) with the advent of heavy, continuous
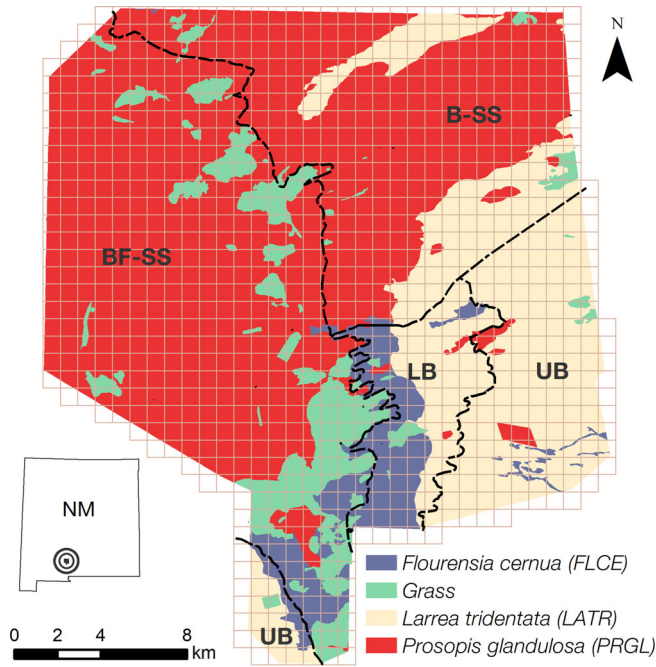
FIGURE 1 Map of the 104,166-ha Jornada Experimental Range and the New Mexico State University Chihuahuan Desert Rangeland Research Center site soil geomorphic units (GMUs) and dominant vegetation in 1998. Grid denotes 805 m × 805 m cells (*n* = 890) whose plant dominance was tracked through time (1858–1998) in this study. Dashed black lines delineate the boundaries of the GMUs that were the focus of this study: upper and lower bajada (UB and LB), bajada sand sheet (B-SS), and basin floor sand sheet (BF-SS). GMUs are from Monger et al. (2006); vegetation map is from Gibbens et al. (2005) who also present vegetation maps of the basin for 1858, 1915–1916, and 1928–1929

livestock grazing. The scenarios differ with respect to hypothetical differences in the occurrence and spatial arrangement of shrubs in the 1850s.

Topoedaphic constraint scenario

Based on historical observations, perennial grasslands would have dominated most of the Jornada Basin. Consistent with historical reports, mesquite shrubs would have been present but confined to deep sandy soils in the northeast part of the basin and to arroyos (steep-sided gullies and channels) dissecting the basin floor (characterized by sandy surface soils with a variable depth to a caliche layer). Creosote bush and tarbush would also have been present within the Jornada Basin, but widely scattered and largely confined to loamy soils on upper bajada (creosote bush) and the finer-textured soils of the lower bajada (tarbush). With the advent of heavy, continuous livestock grazing punctuated by periodic drought, perennial grass cover would have been substantively reduced throughout the entire Jornada Basin (Peters et al., 2015). Under these

conditions, mesquite then expanded laterally from arroyos and across the basin floor, with creosote bush and tarbush proliferating in the upper and lower bajada landscapes, respectively. This scenario assumes the shrub species were present in the historic grassland but confined to specific topoedaphic settings.

Uniform distribution followed by competitive displacement scenario

This scenario assumes that in the 1850s, mesquite, creosote bush, and tarbush shrubs were ubiquitously distributed at low cover/low frequency across the Jornada Basin. With the advent of livestock overgrazing in concert with drought-induced declines in perennial grass cover in the late 1880s, each shrub species would have increased as grass cover decreased. However, the local proliferation of these shrubs would have been differentially promoted or constrained depending upon the physical properties of each soil-GMU. In this scenario, the shrubs in Table 1 were initially sparsely intermingled, but then responded differentially to changes in the disturbance regime to rapidly sort and come to dominate the soil GMUs for which they were best adapted.

Feed-forward scenario

Like the preceding scenario, this scenario presumes a ubiquitous shrub distribution with mesquite proliferating throughout the basin floor with the advent of heavy grazing. However, in this scenario, tarbush initially proliferates across both the upper and lower bajada landscapes, with short-term, grazing-induced erosion further favoring tarbush over grasses. Persistent grazing and longer-term water erosion of fine soils eventually led to a coarsening of the upper bajada soils to create new conditions favoring creosote bush recruitment. These longer-term erosion-induced soil changes would have shifted the recruitment/competitive balance in favor of creosote bush and effected a tarbush-to-creosote bush state change. The translocation of fine soils by water erosion from the upper bajada would have concurrently reinforced tarbush recruitment and persistence on the lower reaches of the bajada. In this scenario, present-day vegetation patterns on the upper/lower bajada would be a consequence of grazing-induced changes in soil properties.

Scenario evaluation

Our focus was the northern Chihuahuan Desert in southern New Mexico, USA, where datasets dating to the

1850s were available to evaluate the above scenarios. Records from 1850s General Land Office township/section surveys and US Forest Service livestock carrying capacity reconnaissance surveys show that perennial grasslands present in the mid-1800s had transitioned to shrublands by the early 1900s at the Jornada Basin USDA Long Term Ecological Research site (Buffington & Herbel, 1965). By 1998, over 90% of the Jornada Basin was shrub-dominated (Gibbens et al., 2005). While this broad-scale change represents a classic grassland-to-shrubland regime shift, we sought to provide a more nuanced view by re-examining the historic data at a finer spatial resolution to ascertain which of the state change scenarios presented earlier might be most plausible.

Approach and objectives

We first gridded the Jornada Basin with 805 m × 805 m cells and classified the dominant vegetation in each of the resulting 890 cells on four dates between 1858 and 1998 using the data described in Buffington and Herbel (1965) and Gibbens et al. (2005). We then computed the frequency of vegetation transitions on each soil-GMU for adjoining (consecutive) time periods. This included the number of cells exhibiting "no change" over a given time interval (e.g., those with the same beginning and ending classifications) and the number of cells that changed from a grass-dominated state to a specific type of shrub-dominated state (or vice versa) over a given time interval. Our objectives were to: (1) assess the extent to which perspectives on vegetation change arising from coarse, basin-scale assessments differ from those derived from finer-scale GMU-specific assessments, (2) use the spatial–temporal transition data to evaluate the plausibility of the three scenarios described earlier, and (3) articulate potential mechanisms and hypotheses that might account for the observed fine-scale variation in vegetation transitions. We were constrained by the dates for which vegetation data were available and recognize that having a different temporal grain (e.g., more dates, different time intervals between dates) could influence our interpretation of the spatial data.

METHODS

Study site

This study was conducted on the Jornada Basin USDA Long Term Ecological Research site (32.5 N, 106.45 W). Long-term (80 years) mean annual precipitation and temperature in the Jornada Basin is 250 mm and 15°C,

respectively. Livestock grazing, which historically was very high and represented overgrazing (Fredrickson et al., 1998), is currently maintained at low levels throughout the Jornada. The Jornada Basin is characterized by contrasting soil GMUs (Monger et al., 2006); we focused on the basin floor sand sheet (BF-SS), the lower and upper bajada (LB and UB, respectively), and the bajada sand sheet (B-SS) (Figure 1). The lower bajada and upper bajada occur in the wind shadow of Summerford Mountain, whereas the bajada sand sheet to the north occurs in an area experiencing higher levels of eolian sand deposition from the basin floor sand sheet (Peters et al., 2011). In this study, perennial grasses, including *Bouteloua eriopoda*, other *Bouteloua* spp., *Pleuraphis mutica*, *Sporobolus* spp., and *Aristida* spp., are collectively called "GRASS"; the main shrub species are mesquite (*P. glandulosa* [hereafter PRGL]), creosote bush (*L. tridentata* [LATR]) and tarbush (*F. cernua* FLCE]) (Table 1). See Havstad et al. (2006) and Peters et al. (2015) for detailed overviews of climate, vegetation, soil GMUs, and natural history.

Vegetation transitions

Fine-scale, decadal-scale transitions in dominant vegetation were assessed via a reanalysis of data used by Buffington and Herbel (1965) and Gibbens et al. (2005) to generate coarse-scale land cover change maps. The original Buffington and Herbel (1965) and Gibbens et al. (2005) 1:32,000 resolution vegetation maps for 1858, 1915, 1928, and 1998 were scanned, digitized in ArcGIS (ESRI v. 10.2; Redlands, CA), and then overlain with a 1:32,000 soil-GMU map (Monger et al., 2006) and a grid comprised of 805 m × 805 m cells. Cells were excluded from analysis when >50% of their area fell outside the Jornada property boundary or beyond the extent of historic vegetation surveys. This process generated a grid of 890 usable cells (57,627 total hectare) whose size represented the coarsest scale of measurement used in the 1858 land surveys conducted along section line intersections and midpoints.

We first constructed a 1858 map of dominant vegetation using shrub presence and grass condition classes (very good, good, fair, or poor) subject to the following rules: (1) A cell was considered grass-dominated in 1858 when cells on the Gibbens et al. (2005) 1858 map were classified as being in "good" or "very good" condition; (2) when grass condition was "fair" or "poor" and a shrub species was present in a cell in 1858, then the cell was considered to be dominated by that shrub species; (3) when grass condition in a cell was "fair" or "poor" and multiple shrub species were present in 1858 based on Gibbens et al. (2005), and only one shrub species was present in the Buffington and Herbel (1965) 1858 map, then

the cell was dominated by the latter shrub species; (4) when grass condition was "fair" or "poor" and multiple shrubs were present in both 1858 maps, then the cell was considered dominated by the dominant shrub on the Gibbens et al. (2005) 1915 map.

Vegetation transition frequencies were computed using an adaptation of the approach described in Scanlan and Archer (1991). The dominant vegetation in each cell of the 1858, 1915, 1928, and 1998 vegetation maps was identified as GRASS, PRGL, LATR, or FLCE (Table 1). We then recorded the number of cells with the same beginning and ending dominant vegetation for three periods (1858–1915, 1915–1928, and 1928–1998). For example, a cell dominated by GRASS at the start of one time period and *P. glandulosa* (PRGL) at the start of the next time period was noted as GRASS-PRGL and a cell dominated by GRASS at the start of one time period and GRASS at the start of subsequent time period would be noted as GRASS. This pair of examples illustrates (1) a cell that transitioned from grass dominance to shrub (PRGL) dominance and (2) a "stationary" cell where grasses remained dominant from one time period to the next (e.g., no change in dominance). Transition pathways were also generated for each cell by combining the transitions from each period to represent the specific sequence of change in dominance between 1858 and 1998. In some instances, the dominant vegetation in a given cell changed multiple times. In those cases, the dominant vegetation was listed in its order of appearance. For example, GRASS-FLCE-PRGL-GRASS would denote a cell that was initially dominated by grass (1858) and subsequently dominated by tarbush (*F. cernua*, FLCE), and then by mesquite (PRGL) before reverting back to grass by 1998. Throughout this paper, we use the term "stationary" to denote cells for which there was no change in dominance from one time period to the next.

The relative frequency of occurrence of the various transition possibilities was calculated as the number of times a transition occurred divided by the total number of grid cells. Transition relative frequencies were computed for the entire Jornada Basin and within each soil-GMU. Transitions occurring in <2% of the cells were grouped as "other."

RESULTS

Basin-scale vegetation transitions (1858–1998)

Initial conditions

Grasses were ubiquitous in 1858, occurring in 62% of the bajada sand sheet cells and in >93% of cells in the other

three GMUs (Table 2b). Similarly, GRASS-dominated cells characterized 84% of all cells in 1858 (Table 2a). By 1998, 91% of these cells had transitioned to shrub dominance on each of the major soil GMUs (Figure 1). PRGL, FLCE, and LATR were present on all soil GMUs within the 1858 Jornada Basin grasslands, but the frequency of occurrence and distribution of dominance of these species varied considerably (Table 2a,b). In all cases, there was a higher frequency of shrubs across the Jornada than expected based on the heretofore assumed close associations between shrub species and soil GMUs. PRGL had a high frequency of occurrence on the bajada sand sheet (83% of cells) and codominated 33% of cells; this shrub species also occurred in moderate frequency on the basin floor sand sheet (52%) but did not dominate any cells. PRGL also occurred at low frequencies on the upper and lower bajada landscape locations. In contrast, LATR and FLCE did not dominate substantial portions of the Jornada landscape in 1858 (<3% and 1% of all cells, respectfully). LATR had a high frequency of occurrence on the upper bajada (99%) and occurred with moderate frequency on the lower bajada (54%) and bajada sand sheet (31%). FLCE was found in high frequencies on both the upper and lower bajada (>84%), and in moderately low frequency on the bajada sand sheet (24%) (Table 2b). Twenty-six other woody species were noted in the historic surveys (see Gibbens et al., 2005), but none ever subsequently increased to achieve dominance.

Vegetation change

Twenty-nine unique vegetation transition combinations (including no change in dominance) occurred in the Jornada Basin from 1858 to 1998. Seven transitions were common to 88% of cells (Table 2c). The remaining 22 transitions never exceeded 2% of cells (range = 0.1%–2%). GRASS-PRGL was the primary shrub transition (47% of cells), followed by GRASS-FLCE-LATR transitions (15%). PRGL-dominated states were the most stable (10% of cells starting in this state remained in it), and PRGL was dominant in one or more periods in 57% of cells. Stable LATR-dominated states were initially uncommon (stationarity exhibited on only 0.2% of cells) but increased in frequency as dominance shifted away from GRASS- and FLCE-dominated areas (2.6% and 15.4%, respectively). Shrub states initially dominated by FLCE were highly transient (stationarity exhibited in 0% of transitions), typically giving way to LATR on upslope areas. Transitions from shrub dominance back to GRASS dominance also occurred but were uncommon (LATR-FLCE-GRASS = 0.2% of transitions; PRGL-GRASS = 0.2%; GRASS-FLCE-PRGL-GRASS = 0.1%; and

TABLE 2 (a) Number of grass- and shrub-dominated cells in contrasting soil geomorphic units in 1858, (b) presence of present-day dominant shrub species in 1858, and (c) vegetation transition pathways (count [number of cells] and frequency of occurrence [*F*, %]) on four contrasting soil geomorphic units in the Chihuahuan Desert Jornada Basin representing the combined sequence of dominant vegetation transitions across all dates (1858, 1915, 1928, 1963, and 1998)

Species	Soil geomorphic unit				Total no. cells	*F* (%)
	Lower bajada	Upper bajada	Bajada sand sheet	Basin floor sand sheet		
No. cells (% of total)	97 (10.9)	85 (9.6)	332 (37.3)	376 (42.2)	890	100
(a) Dominance in 1858						
FLCE	1 (1.0)	2 (2.4)	6 (1.8)	0 (0)	9	1.0
GRASS	89 (91.8)	83 (97.7)	198 (59.6)	376 (100)	746	83.8
LATR	7 (7.2)	0 (0)	19 (5.7)	0 (0)	26	2.9
PRGL	0 (0)	0 (0)	109 (32.8)	0 (0)	109	12.2
(b) Presence in 1858						
FLCE	83 (85.6)	71 (83.5)	79 (23.8)	27 (7.2)	260	29.2
GRASS	90 (92.8)	83 (97.7)	205 (61.8)	376 (100)	754	84.7
LATR	52 (53.6)	84 (98.8)	103 (31.0)	2 (0.5)	241	27.1
PRGL	9 (9.9)	2 (2.4)	275 (82.8)	196 (52.1)	482	54.2
(c) Transition pathway						
FLCE[a]	…	…	…	…	…	…
GRASS	5 (5.2)	…	…	56 (14.9)	61	6.9
GRASS-FLCE	33 (34)	…	…	24 (6.4)	57	6.4
GRASS-FLCE-LATR	39 (40.2)	67 (78.8)	29 (8.7)	2 (0.5)	137	15.4
GRASS-LATR	1 (1)	14 (16.5)	8 (2.4)		23	2.6
GRASS-PRGL	4 (4.1)	…	118 (35.5)	292 (77.7)	414	46.5
LATR	1 (0.3)	…	1 (0.3)	…	2	0.2
PRGL	…	…	92 (27.7)	…	92	10.3
Other[b]	15 (15.5)	4 (4.7)	85 (25.6)	2 (0.5)	106	11.9
Totals	97 (100)	85 (100)	332 (100)	376 (100)	890	100
No. stable, no-change cells	2	0	2	1		
No. dominance transitions	12	5	21	5		

Note: "GRASS" represents all perennial C_4 species (see *Study site*). In (c), species dominance in transitions is given in sequential (earliest to latest) order (PRGL = *Prosopis glandulosa*; LATR = *Larrea tridentata*; and FLCE = *Flourensia cernua*); rows with only PRGL or GRASS denote cells where that vegetation dominated on all dates.

[a]There were no stable, "no-change" FLCE cells.

[b]Transitions occurring in <2% of cells; includes two LATR stable, no-change cells: one on bajada sand sheet and one in lower bajada.

GRASS-PRGL-GRASS = 0.1%) (these are included in the "Other" transitions in Table 2c). Across all time periods, GRASS stationarity occurred only on the basin floor sand sheet and lower bajada GMUs (15% and 5% of cells, respectively). PRGL stationarity was observed only on the bajada sand sheet (28% of cells). Stationarity of LATR was extremely low (observed only on the bajada sand sheet and in <2% of cells); FLCE exhibited no stationarity on any soil GMUs. The bajada sand sheet and lower bajada exhibited the largest variety of transitions (21 and 12, respectively). The variety of transitions on the upper bajada (5) and basin floor sand sheet (5) was low and comparable to each other.

Vegetation transitions on soil GMUs

For all three time periods, GRASS stationarity was highest on the basin floor sand sheet and lowest on the upper bajada and bajada sand sheet GMUs (Figure 2).
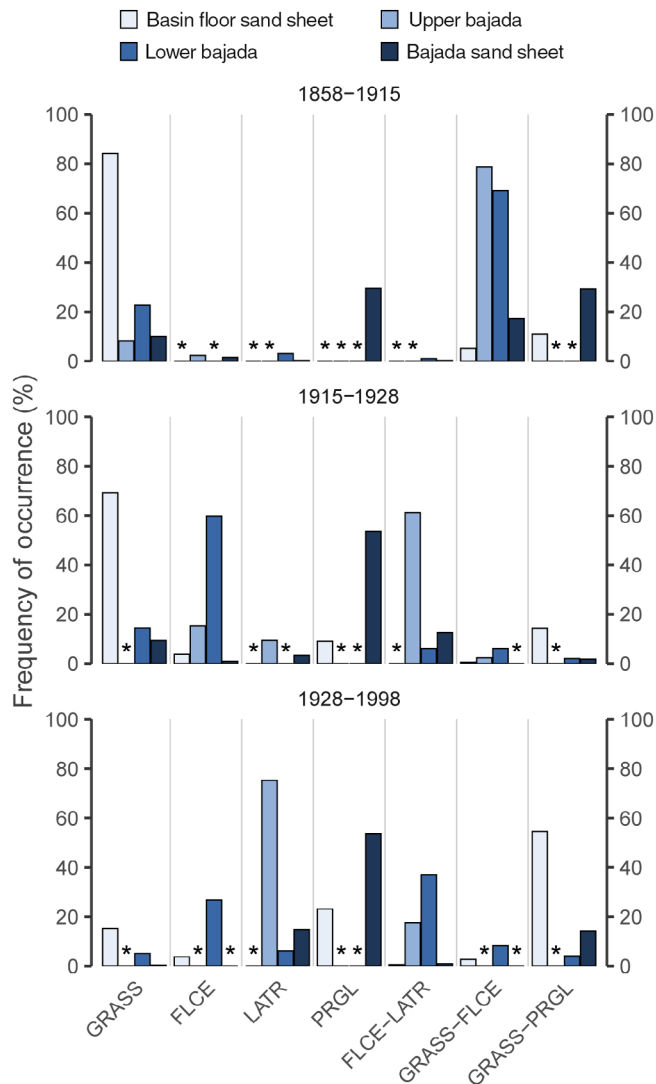
FIGURE 2 Frequency of occurrence (*F*, %) of plant dominance transitions occurring on the basin floor sand sheet, the lower and the upper bajada, and bajada sand sheet soil geomorphic units (GMUs) over three time intervals (1858–1915, 1915–1928, and 1928–1998). *F* was independently calculated for each geomorphic unit; only transitions with *F* > 20% are shown. Species dominance is given in sequential (earliest to latest) order; single species codes represent stationarity (no change in dominance). Asterisks (*) denote transitions not observed for a given soil-GMU and time period; gaps for a given GMU represent low values. See Table 2 legend for species codes; see Tables 3–6 for listing of all transitions and their frequencies of occurrence

GRASS-FLCE transitions predominated in the upper bajada and lower bajada between 1858 and 1915, giving way to FLCE-LATR transitions in the subsequent time periods. FLCE stationarity was highest on the lower slopes of the bajada after 1915. LATR stationarity was highest on the upper reaches of the bajada after 1928. GRASS-PRGL transitions were prominent relatively early on the bajada sand sheet (between 1858 and 1915) and

TABLE 3 Number of cells and percent frequency of occurrence (in parentheses) for all transitions recorded on the basin floor sand sheet soil geomorphic unit (see Figure 1) illustrate the temporal heterogeneity and diversity in dominant vegetation change

Transitions	1858–1915	1915–1928	1928–1998
FLCE		14 (3.7)	14 (3.7)
FLCE-GRASS		5 (1.3)	
FLCE-LATR			2 (0.5)
GRASS	316 (84.0)	260 (69.1)	57 (15.2)
GRASS-FLCE	19 (5.1)	2 (0.5)	10 (2.7)
GRASS-PRGL	41 (10.9)	54 (14.4)	205 (54.5)
PRGL		34 (9.0)	87 (23.1)
PRGL-GRASS		7 (1.9)	1 (0.3)
No. stable, no-change cells	1	3	3
No. dominance transitions	2	4	4

Note: Species dominance is given in sequential (beginning and ending) order for each interval between vegetation surveys (see Table 2 footnotes for species codes).

later (1928–1998) on the basin floor sand sheet. Tables 3–6 6 in the following sections provide additional details on all transitions observed for GMUs in each time period.

The diversity of observed transitions in dominance in the first time period was highest in the bajada sand sheet GMU (9 different transitions) and lower and comparable among the other GMUs (2 or 3) (Figure 3). The number of transitions observed in the bajada sand sheet continued at a high level in each of the subsequent time periods (10 and 8, respectively), and increased markedly in the lower bajada (to 7 and 8) and only slightly in the upper bajada and basin floor sand sheet (4–5 distinctive transitions).

GRASS-to-shrub transitions dominated between 1858 and 1998, but grass–shrub–grass transitions were also observed on each of the Jornada Basin soil GMUs, albeit at low (<5%) frequencies (Tables 3–6). FLCE-GRASS transitions were the most common and occurred on each of the GMUs, primarily between 1915 and 1928. LATR-GRASS transitions were observed on the bajada sand sheet and lower bajada; PRGL-GRASS transitions occurred on the basin floor sand sheet and bajada sand sheet.

Basin floor sand sheet

Basin floor sand sheet cells (*N* = 376) were grass-dominated in 1858 (100% of cells; Table 2a,b). Cells

TABLE 4 Number of cells and percent frequency of occurrence (in parentheses) for all transitions on the bajada sand sheet soil geomorphic unit (Figure 1) illustrate the temporal heterogeneity and diversity in dominant vegetation change

Transitions	1858–1915	1915–1928	1928–1998
FLCE	5 (1.5)	3 (0.9)	
FLCE-GRASS		14 (4.2)	
FLCE-LATR	1 (0.3)	42 (12.7)	3 (0.9)
FLCE-PRGL		20 (6.0)	3 (0.9)
GRASS	33 (9.9)	31 (9.3)	1 (0.3)
GRASS-FLCE	57 (17.2)		
GRASS-LATR	11 (3.3)		11 (3.3)
GRASS-PRGL	97 (29.2)	6 (1.8)	47 (14.2)
LATR	1 (0.3)	11 (3.3)	49 (14.8)
LATR-FLCE	14 (4.2)	2 (0.6)	
LATR-GRASS		1 (0.3)	2 (0.6)
LATR-PRGL	4 (1.2)	3 (0.9)	9 (2.7)
PRGL	98 (29.5)	178 (53.6)	178 (53.6)
PRGL-FLCE	3 (0.9)	1 (0.3)	
PRGL-GRASS	4 (1.2)	13 (3.9)	2 (0.6)
PRGL-LATR	4 (1.2)	7 (2.1)	27 (8.1)
No. stable, no-change cells	4	4	3
No. dominance transitions	9	10	8

Note: Species dominance is given in sequential (beginning and ending) order (see Table 2 footnotes for species codes).

TABLE 5 Number of cells and percent frequency of occurrence (in parentheses) for all transitions on the lower bajada soil geomorphic unit (Figure 1) illustrate the temporal heterogeneity and diversity in dominant vegetation change

Transitions	1858–1915	1915–1928	1928–1998
FLCE		58 (59.8)	26 (26.8)
FLCE-GRASS		5 (5.2)	2 (2.1)
FLCE-LATR	1 (1.0)	6 (6.2)	36 (37.1)
FLCE-PRGL		2 (2.1)	1 (1.0)
GRASS	22 (22.7)	14 (14.4)	5 (5.2)
GRASS-FLCE	67 (69.1)	6 (6.2)	8 (8.2)
GRASS-LATR			5 (5.2)
GRASS-PRGL		2 (2.1)	4 (4.1)
LATR	3 (3.1)		6 (6.2)
LATR-FLCE	4 (4.1)	1 (1.0)	
LATR-GRASS		3 (3.1)	
PRGL-FLCE			1 (1.0)
PRGL-LATR			3 (3.1)
No. stable, no-change cells	2	2	3
No. dominance transitions	3	7	8

Note: Species dominance is given in sequential (beginning and ending) order (see Table 2 footnotes for species codes).

exhibiting GRASS stationarity declined steadily over the three subsequent time periods (from 84% to 69% to 15%) (Table 3). During the 1858–1915 period, GRASS gave way to either PRGL (11% of cells) or FLCE (5% of cells) dominance. GRASS-PRGL transitions continued, slightly increasing in 1915–1928 (14.4% of cells) and substantially increasing during the 1928–1998 period (54.5% of cells); GRASS-FLCE transitions also occurred during these time intervals, but at much lower frequencies (0.5% and 2.7% of cells, respectively). By 1998, 77.7% of cells on the basin floor sand sheet were dominated by PRGL. Shrub-to-GRASS transitions were observed subsequent to 1915, but with low frequencies (FLCE-GRASS = 1.3% of cells; PRGL-GRASS = 1.9% and 0.3% of cells in 1915–1928 and 1928–1998, respectively). The number of distinct dominance transition pathways on the basin floor sand sheet increased from two in 1858–1915 to four in 1915–1928 and 1928–1998 (Table 3).

TABLE 6 Number of cells and frequency of occurrence (%, in parentheses) for all transitions on the upper bajada soil geomorphic unit (Figure 1) illustrate the temporal heterogeneity and diversity in dominant vegetation change

Transitions	1858–1915	1915–1928	1928–1998
FLCE	2 (2.4)	13 (15.3)	
FLCE-GRASS		4 (4.7)	
FLCE-LATR		52 (61.2)	15 (17.6)
FLCE-PRGL			1 (1.2)
GRASS	7 (8.2)		
GRASS-FLCE	67 (78.8)	2 (2.4)	
GRASS-LATR	9 (10.6)	5 (5.9)	4 (4.7)
LATR		8 (9.4)	64 (75.3)
LATR-FLCE		1 (1.2)	
LATR-PRGL			1 (1.2)
No. stable, no-change cells	2	2	1
No. dominance transitions	2	5	4

Note: Species dominance is given in sequential (beginning and ending) order (see Table 2 footnotes for species codes).
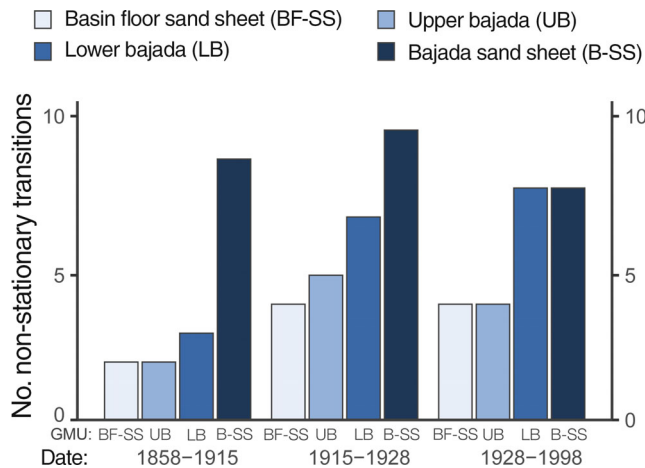
FIGURE 3 Number of unique vegetation dominance transitions occurring on contrasting soil geomorphic units (basin floor sand sheet, lower and upper bajada, and bajada sand sheet) within the 104,166-ha Jornada Basin study site on three consecutive time periods (1858–1915, 1915–1928, and 1928–1998). See Tables 3–6 for listing of transitions

Bajada sand sheet

The 1858 bajada sand sheet was a mixture of cells dominated by GRASS (60%) and cells dominated by PRGL (33%) (Table 2). GRASS stationarity was comparable during the 1858–1915 and 1915–1928 time periods (10% and 9% of cells, respectively), but declined an order of magnitude to 0.3% during the 1928–1998 period (Table 4). The proliferation of woody plants during the 1858–1915 period (nine unique transitions) resulted in more than 83% of GRASS cells transitioning to shrub-dominated states. PRGL-PRGL, GRASS-PRGL, and GRASS-FLCE transitions (30%, 29%, and 17% of cells, respectively) were most frequently observed during this period, which also included a few GRASS-LATR transitions (3% of cells). Cells exhibiting PRGL stationarity dominated in the 1915–1928 and 1928–1998 periods (53.6% and 53.6% of cells, respectively). PRGL inroads during the 1915–1928 period were small (GRASS-PRGL = 1.8% of cells), then increased substantively between 1928 and 1998 (GRASS-PRGL = 15% of cells). However, the 1928–1998 increases in PRGL dominance were offset by PRGL-LATR transitions occurring in 8% of cells. Shifts from shrub-to-GRASS dominance were infrequent (<4% in any given time period), varied from period to period, and occurred for all three shrubs: PRGL, LATR, and FLCE.

Lower bajada

The 1858 lower bajada ($N = 97$ cells) was characterized by GRASS (91.8% of cells) dominance with low frequencies of LATR and FLCE (7.2% and 1.0%, respectively; Table 2). As with the basin floor sand sheet, cells exhibiting GRASS stationarity declined steadily in the three subsequent time periods (from 22.7% to 14.4% to 5.2% of cells) (Table 5). During the 1858–1915 period, FLCE achieved widespread dominance owing to transitions from GRASS to FLCE (69.1% of cells); this was accompanied by LATR-FLCE transitions (4.1% of cells) that were somewhat offset by FLCE-LATR transitions (1.0% of cells). The subsequent 1915–1928 period was characterized by FLCE and GRASS stationarity (59.8% and 14.4% of cells, respectively), additional FLCE displacement of grasses (6.2% of cells), and an array of shrub–shrub transitions with frequencies ranging from 1.0% to 6.2%. During the 1928–1998 period, FLCE displacement of grasses continued (8.2% of cells), but these increases in FLCE were substantially offset by pronounced shifts from FLCE-to-LATR dominance elsewhere in the lower bajada (37.1% of cells). Transitions from shrub dominance back to grass dominance were observed subsequent to 1915, but with low frequencies (FLCE-GRASS = 5.2% and 2.1% of cells in 1915–1928 and 1928–1998, respectively; LATR-GRASS = 3.1% of cells, only in 1915–1928). Transitions in dominance occurring in the lower bajada increased from three in 1858–1915 to seven in 1915–1928 and eight in 1928–1998 (Table 5).

Upper bajada

Cells on the upper bajada soil GMUs were dominated by GRASS in 1858 (98% of cells; $N = 83$; Table 2). These cells subsequently exhibited 10 different transition pathways over the three time periods between 1858 and 1998, with most transitions in dominance occurring in the 1915–1928 and 1928–1998 time periods (5 and 4, respectively) (Table 6). GRASS-FLCE transitions predominated during the 1858–1915 period (79% of cells), with FLCE dominance giving way to LATR dominance in the subsequent 1915–1928 period (61% of cells). These LATR-dominated ecosystems persisted through the 1928–1998 period (75% of cells) and were joined by an additional 15 cells (18%) that transitioned from FLCE to LATR and 4 cells that transitioned from GRASS to LATR. All told, 98% of cells on the upper bajada transitioned to LATR dominance between 1858 and 1998. Pathways that included multiple shrub-dominated states occurred in 81% of cells. Pathways representing transitions from GRASS to LATR that included an intermediate FLCE-dominated period occurred most frequently (79%) with only 17% of cells transitioning directly from a GRASS-to-LATR dominance (Table 2c). Transitions involving PRGL occurred in only two upper bajada cells (one FLCE-PRGL and

one LATR-PRGL), both during the 1928–1998 interval. This transition type occurred only on cells that were subjected to "brush management," which apparently interfered with dominant processes governing vegetation change.

DISCUSSION

Desertification has primarily focused on state changes from perennial grasslands to shrub-dominated vegetation. The shrublands replacing grasslands in drylands are typically assumed to be stable. We examined this assumption using long-term, decadal-scale vegetation data from a northern Chihuahuan Desert site. Below, we summarize the extent to which fine- versus coarse-scale perspectives influence perceptions of vegetation change (Objective 1), evaluate the plausibility of the three scenarios presented in Section "Introduction" (Objective 2), and propose potential mechanisms and hypotheses that might account for or shed light on the changes in vegetation that we observed (Objective 3). We note that our interpretations are constrained by the fact that we had only four dates of vegetation maps and that the time intervals between maps varied.

Coarse- versus fine-scale perspectives on vegetation change

Long-term (1953–2009), fine-scale transect data from the Sonoran Desert suggest that vegetation transitions are not necessarily strongly constrained by soils and topography and that propensities for state transition in a given setting may depend on the traits of key species (Bagchi et al., 2012). Our analyses of historic Jornada Basin data at a coarse basin-scale resolution over the 140-year period revealed relatively few and simple transitions. Perennial grasslands transitioned to their current, relatively stable shrub-dominated states consistent with traditional models of grassland-to-shrubland transitions. However, this coarse-scale perspective masked the high frequency and diversity of state transitions occurring within GMUs and involving contrasting shrub functional types over shorter time frames. The coarse-scale simplification of state transitions potentially obscures underlying mechanisms explaining processes driving transition dynamics. Our fine-scale assessments of individual GMUs over discrete time intervals do not consistently support a single explanation for grassland-to-shrubland transitions. Indeed, our analyses suggest state transition drivers are spatially and temporally variable, both within and between GMUs.

Competing scenarios of grassland-to-shrubland state transitions

Competing scenarios accounting for grassland-to-shrubland state change presented in Section "Introduction" differ primarily with respect to assumptions regarding the initial distributions of shrub species. Individuals of the three currently prominent shrub species represent markedly different functional groups (Table 1). These shrub species were present across the basin in low frequencies of occurrence in 1858 (Buffington & Herbel, 1965; Gibbens et al., 2005). Our fine-scale analysis confirmed that the three main shrub species occurred on each of the basin GMUs in 1858, though with different frequencies (e.g., PRGL with highest frequencies on the sandy basin floor and bajada sand sheet; LATR and FLCE with highest frequencies on the upper and lower bajada, respectively) (Table 2b). This challenges traditional assumptions that shrub species were initially spatially segregated based on landscape position. Our analyses suggest that with grazing- and drought-induced reductions in grass cover and associated soil erosion, PRGL preferentially proliferated from the basin floor and bajada sand sheets, with FLCE preferentially proliferating across the bajada. By 1915, PRGL dominated much of the bajada sand sheet and FLCE much of the lower and upper bajada, with GRASS still predominating on the basin floor sand sheet. As livestock overgrazing continued and its effects were amplified by periodic, multiyear drought (Fredrickson et al., 1998), PRGL continued to proliferate on the basin floor sand sheet. By 1998, PRGL had largely displaced GRASS on this GMU. The trend on the upper bajada was quite different, wherein FLCE did not increase or even persist in dominance subsequent to 1915, but rather was replaced by LATR. Given this spatiotemporal complexity, the generalization that "grasslands transitioned to shrublands" overlooks and masks important details that have implications for understanding ecosystem structure and function and for predicting future states. In the following sections, we use these finer-scale spatiotemporal perspectives to propose hypotheses regarding the mechanisms and processes underlying shrubland state change.

Hypotheses and mechanisms

The upper and lower bajada cases

The bajada best exemplifies a deviation from the traditional model of grassland-to-shrubland transition and is consistent with the feed-forward scenario described in the "Introduction". The three shrub species dominating

today's landscapes were present in the upper and lower bajada grasslands in 1858 with each dominating a small percentage of the cells. The upper bajada subsequently transitioned to a landscape almost exclusively dominated by LATR. However, transitions from GRASS to LATR in this portion of the landscape typically included an intermediate stage of FLCE dominance. Generally, upslope cells on the bajada experienced a more rapid and extensive transition to LATR, whereas downslope portions lagged behind and were more spatially heterogeneous (data not shown). Toward the lower bajada, FLCE remained relatively stable between 1928 and 1998, and continues to dominate present-day (2021) landscapes.

Alternate hypotheses for the GRASS-FLCE-LATR sequence center around (1) FLCE having better seed production, seed dispersal, and/or seedling establishment capabilities than LATR that would give it an advantage in proliferating in grazed grasslands, (2) FLCE modifying soils and microclimate subsequent to its establishment to facilitate LATR recruitment, and (3) LATR competitively excluding FLCE subsequent to its establishment. This general sequence of events involving multiple shrub functional groups has been documented in other systems (Archer, 1995).

Hypotheses centered around changes in soil properties would also be consistent with our field observations. The arrangement of soils along the long (~10 km), gently sloping (1%–3%) bajada gradient is principally driven by surficial water erosion (Gile, 1981; Monger & Bestelmeyer, 2006). We therefore hypothesize that the observed shift from FLCE to LATR was a consequence of grazing-induced acceleration of the water erosion of fines on the upper bajada slopes that led to a coarsening of surficial soils and the development of conditions more suitable for LATR seedling recruitment and growth. This change in soil texture could have shifted the competitive balance in favor of creosote bush and led to the observed FLCE-LATR state change on the upper bajada. The translocation of fine-textured soils by water would have concurrently reinforced FLCE persistence on the lower bajada, where it has maintained its dominance. This hypothesis is consistent with the differential responses of FLCE and LATR to soil texture (Table 1). The relatively rapid transition from FLCE to LATR between 1915 and 1928 (1) is consistent with the fact that FLCE is relatively short-lived (Table 1), (2) suggests the possibility of infrequent events driving rapid, nonlinear (as opposed to gradual, linear) transitions from one shrub type to another via episode(s) imparting differential mortality/recruitment in conjunction with episodes of accelerated erosion, or (3) is an artifact of the temporal spacing of sampling dates or the spatial resolution of the maps that may favor one shrub species or another.

The basin floor and bajada sand sheet case

Traditional models of grassland-to-shrubland transition generally suffice to explain GRASS-PRGL transitions on the basin floor and bajada sand sheets. The three shrub species dominating today's Jornada Basin landscapes were also present on the grasslands dominating these GMUs in 1858 (Table 2b). Interestingly, PRGL dominated 32.8% of the cells on the bajada sand sheet at this time, ostensibly reflecting activities of indigenous peoples on these landscapes (Fredrickson et al., 2006) or long-term dominance of this species on this landform. GRASS-PRGL transitions between 1858 and 1915 were primarily on the bajada sand sheet (Figure 2), perhaps reflecting the higher frequency of occurrence of PRGL there (82.8% of cells) compared with the basin floor (52.1% of cells) (Table 2b). Interestingly, GRASS-PRGL transitions diminished in the 1915–1928 period on both GMUs, then increased again in the 1928–1998 period where they were primarily on the basin floor. This lull in transitions on the basin floor and bajada sand sheets contrasts the pronounced increase in FLCE-LATR transitions on the bajada GMUs at this time. We are challenged to explain this within-basin variation in state transition rates and dynamics.

Broader implications

Spatiotemporal variation in state transitions

The number of transition pathways in bajada sand sheet GMU (range = 8–10) and lower bajada (range = 3–8) exceeded that in the upper bajada GMU (range = 2–5) and basin floor sand sheet (range = 2–4). Since this accounting of transitions was based on shifts in dominance occurring in 0.8 × 0.8 km cells, the number of transitions is, in effect, an assessment of within-GMU spatial variation in vegetation dynamics. Why might spatial heterogeneity in plant functional type dominance be so high in the bajada sand sheet and lower bajada compared with the basin floor sand sheet and upper bajada GMUs? One working hypothesis would center around connectivity-based GMU interactions, wherein eolian transport of sand from the basin floor interacts with the water transport of fines from upper to lower reaches of the bajada. This hypothesis is suggested by the observation that the lower bajada lies in the wind shadow of Mt. Summerford, whereas the bajada sand sheet occurs beyond that wind shadow (Monger et al., 2006). Thus, while vegetation on both the lower bajada and bajada sand sheet landscapes would experience the redistribution of resources associated with grazing-induced

modifications of downslope water flow over decadal scales (e.g., of water, nutrients, seeds, soils), vegetation on the bajada sand sheet would experience additional resource redistributions from other GMUs owing to its direct exposure to seasonally strong prevailing winds. This grazing–wind–water interaction could therefore manifest itself in (1) a high spatial heterogeneity of transitions in vegetation dominance where all three are in play and (2) the creation of conditions in one portion of the regional landscape that would favor some shrub functional groups over others.

Furthermore, qualitative inspections of aerial imagery and ground-based measurements indicate more complex vegetation patterning on the lower bajada compared with that on the other soil GMUs. These patterns on the lower bajada, which include labyrinths of vegetated bands (10–50 m width) and gaps/bare spots 5–20 m in diameter, are analogous to those of banded vegetation occurring in arid and semiarid regions globally on locations with gentle slopes (<0.2%) and mean annual rainfall ranging from 200 to 550 mm year^{-1} (Rietkerk et al., 2002). At the Jornada, these complex spatial patterns appear to be a long-term manifestation of downslope water movement of soil and seeds interacting with upslope eolian vectors (Weems & Monger, 2012). Disturbances associated with historic livestock grazing superimposed over this topoedaphic template of co-occurring upslope (wind)/downslope (water) transport vectors would further amplify vegetation dynamics and patterns to influence the rates and dynamics of vegetation change (Monger et al., 2015).

"Shrub" encroachment

The term "shrub" encompasses a wide range in woodiness and stature, ranging from short-statured, herb-like "sub-shrubs" and "half-shrubs" to prototypic multi-stemmed fruticose growth forms, to arborescent. The treatment of "shrubs" as a de facto functional group befits investigation of woody plant encroachment into grasslands as a global phenomenon but ignores the fact that relatively few woody species in a regional flora have become aggressive encroachers. The questions as to what functional traits have enabled some shrubs to proliferate in grasslands over the past 150 years while others have not remain open (Archer et al., 2017). The dominant three shrub species at our study site and the functional groups they represent (Table 1) are but a small fraction of the Basin's shrub flora (26 woody species have been recorded in historic surveys; see Gibbens et al., 2005). The transitions from one shrub functional type to another on the bajada raise questions as to what

shrublands may look like under future climate and disturbance regimes as the present-day dominants progress through their life cycles or respond to a disturbance. For example, the 1998 bajada was clearly dominated by LATR. However, recent vegetation inventories of a watershed in the upper bajada (Templeton et al., 2014) revealed dominance by *Parthenium incanum* (Asteraceae) and secondary codominance by PRGL and LATR. *P. incanum* is a small, drought-tolerant evergreen shrub mentioned in passing in the "other shrubs" category in the 1915 survey (Gibbens et al., 2005). Is *P. incanum* indicative of a new, in-progress shrubland-to-shrubland state change on this GMU? Does the abundance of PRGL in this watershed represent an in-progress increase in a deep-rooted, deciduous N_2-fixing shrub (PRGL) and foreshadow a displacement of an evergreen xerophyte (LATR) on the bajada? Will there be future shrubland-to-shrubland transitions on the other GMUs? Additional long-term data and monitoring are needed to answer these questions.

SUMMARY AND CONCLUSIONS

Arid and semiarid landscapes are often characterized by desertification, wherein landscapes have transitioned from perennial grasslands to shrublands. These transitions are typically represented as being straightforward, and the shrublands developing on former grasslands are traditionally viewed as being stable. We challenged these paradigms using a fine-scale analysis of 1858, 1915, 1928, and 1998 vegetation maps to evaluate three alternative pathways of shrubland state transitions.

We found that shrubland states developing on former grasslands were spatially and temporally more dynamic than has been generally presumed. Livestock overgrazing combined with periodic multiyear drought reduced perennial grass cover throughout our study area. Tarbush increased on bajadas, whereas mesquite increased on the sandy basin floor and bajada sand sheet landforms. However, while mesquite proliferation continued in the sandy landscape components in subsequent decades, grazing-induced soil erosion on the upper bajada appears to have enabled creosote bush to displace tarbush and attain dominance. In the meantime, translocation of fine soil particles to lower bajada landscape elements reinforced tarbush dominance on those landscape elements. The shrubs invading the Chihuahuan Desert grasslands (mesquite, tarbush, and creosote bush) represent contrasting shrub functional types. Accordingly, characterizing observed changes as simply a "grassland-to-shrubland" state change ignores spatiotemporal complexities that will have consequences for primary production,

plant–soil feedbacks, nutrient cycling, biodiversity, and trophic interactions.

The dynamics of the shrublands developing on former grasslands has received little attention. Our data illustrate how "grassland-to-shrubland" state transitions should be refined to recognize and accommodate shrubland–shrubland state changes involving shifts in contrasting woody plant functional groups. Understanding the mechanisms and drivers of transitions between shrub states defined by woody plant functional attributes will be germane to predicting the direction, magnitude, likelihood, and consequences of future changes in shrubland states.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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