The Grassland–Shrubland Regime Shift in the Southwestern United States: Misconceptions and Their Implications for Management

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Transitions from semiarid grassland to shrubland states are among the most widely recognized examples of regime shifts in terrestrial ecosystems. Nonetheless, the processes causing grassland–shrubland transitions and their consequences are incompletely understood. We challenge several misconceptions about these transitions in desert grasslands, including that (a) they are currently controlled by local livestock grazing and drought events, (b) they represent severe land degradation, and (c) restoration of grassland states is impossible. Grassland–shrubland transitions are the products of multiple drivers and feedback systems, both ecological and social, interacting at multiple scales of space and time. Grass recovery within shrubland states—with and without shrub removal—produces novel ecosystems that are dissimilar from historical grasslands but that provide important ecosystem services. Projected increases in climate variability are likely to promote the further displacement of perennial grasses by xerophytic shrubs. This article offers guidelines for managing grassland–shrubland transitions in the face of changing biophysical and socioeconomic circumstances.

Keywords: long-term data, novel ecosystems, restoration, social–ecological, state transition, threshold

Regime shifts are large, persistent changes in ecosystem structure and function (Biggs et al. 2012). Classic examples include the eutrophication of lakes, the collapse of fisheries, and the transition from hard coral to algal dominance in reef systems (Rocha et al. 2015). These changes can significantly alter ecosystem services, imperil biodiversity, and disrupt human livelihoods. Consequently, there is great interest in developing general approaches for both avoiding and adapting to regime shifts, capitalizing on the notion that a diverse array of cases share common characteristics and indicators (Scheffer 2009).

Because of their fragility and broad distribution, arid to semiarid grasslands and savannas have featured prominently in thinking about regime shifts (D'Odorico et al. 2012, Scheffer et al. 2015). Perennial grasslands and savannas can undergo persistent, widespread transitions to shrublands or woodlands featuring reduced or no grass cover (Folke et al. 2004, Bestelmeyer et al. 2006a). Globally, the proliferation of woody plants is triggered by drivers that reduce grasses preferentially over woody plants (e.g., overgrazing by livestock), that eliminate disturbances that favor grasses over woody plants (e.g., reductions in fire frequency), or that favor C3 woody plants over C4 grasses (e.g., rising atmospheric carbon dioxide levels; Archer et al. 2017). Changes in driver levels can initiate feedback loops that accelerate woody-plant recruitment and growth alongside grass loss (D'Odorico et al. 2012). In arid grasslands, soil erosion and nutrient redistribution that favor shrubs and impede grass recruitment and persistence are important feedback mechanisms (Schlesinger et al. 1990, Li et al. 2007, Alvarez et al. 2012). When these feedback mechanisms are initiated, transitions back to former states cannot be reversed simply by relaxing the driver (e.g., grazing pressure) because of "hysteresis" effects (Scheffer et al. 2001). When feedback-driven transitions are difficult or impossible to reverse, the system is said to have crossed a *critical threshold*, and the transition is categorized as a *regime shift* (Biggs et al. 2012), particularly when such transitions occur at broad spatial scales (Levin and Möllmann 2015). Because grassland–shrubland transitions are associated with a loss of livestock forage, increased soil erosion, and diminished air quality, they are often interpreted as a form of land degradation, specifically *desertification* (Geist 2005, Peters et al. 2013). However, the causes, impacts, and reversibility of grassland–shrubland transitions

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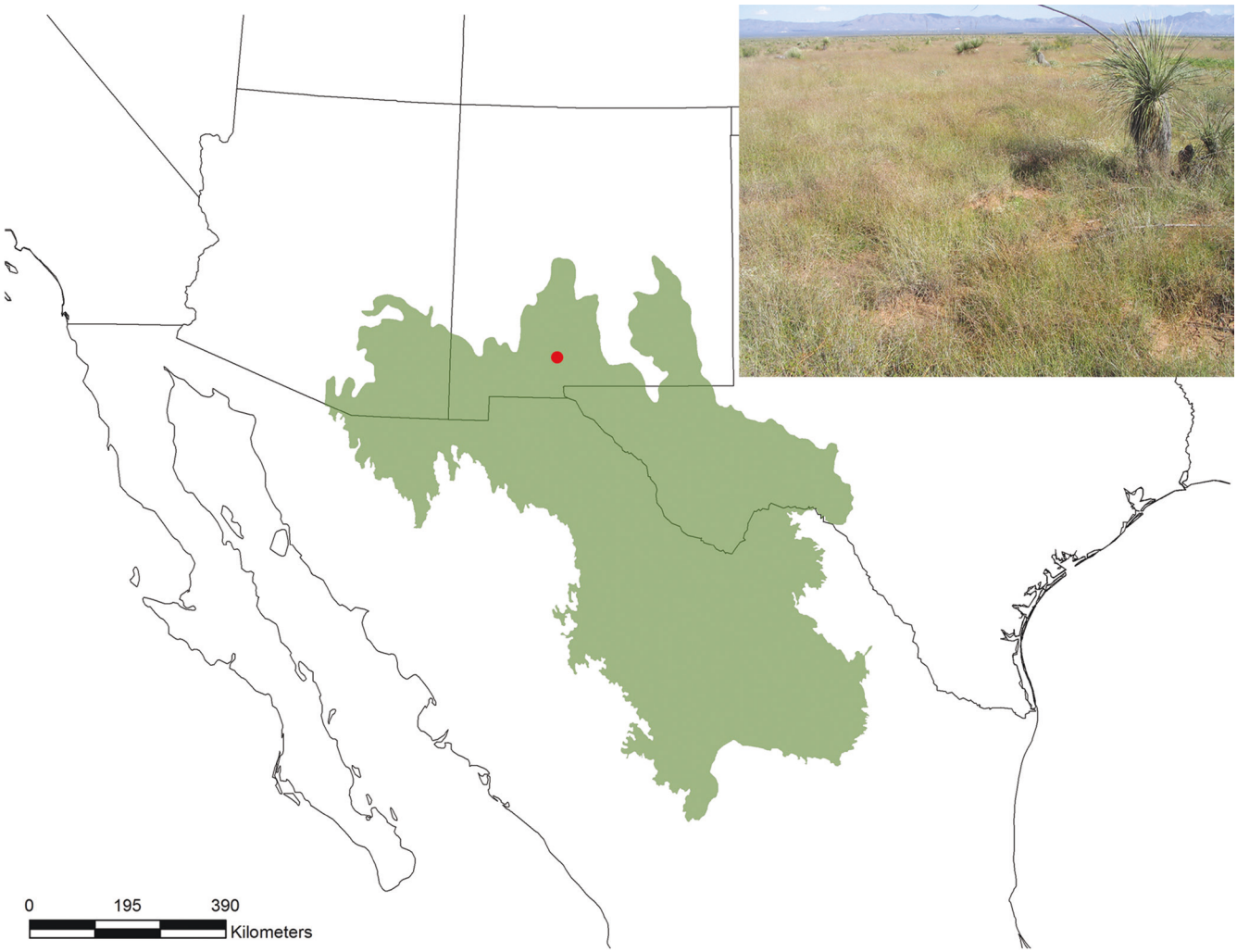

Figure 1. The approximate extent of the North American desert grassland region, with the location of the Jornada Experimental Range/Jornada Basin LTER site (red dot). The inset image is a reference grassland state.

vary widely among grasslands around the globe (Maestre et al. 2009a, Eldridge et al. 2011, Archer et al. 2017), leading to inconsistent and sometimes conflicting environmental narratives.

Regime shifts and desertification are often presented as abstractions, sometimes formalized by conceptual or mathematical models (Walker et al. 1981, Schlesinger et al. 1990, Anderies et al. 2002, van Langevelde et al. 2003). Such abstractions are necessary steps to develop general approaches for understanding and predicting regime shifts, but they can also oversimplify and potentially misrepresent the nature of regime shifts in specific ecosystems and undermine sound management if applied uncritically. In this article, we use a century-long body of evidence from the US Department of Agriculture Jornada Experimental Range (JER) and Jornada Basin Long Term Ecological Research (LTER) site and surrounding areas within the Chihuahuan Desert grassland region of the southwestern United States to provide an empirical perspective on grassland–shrubland transitions. We use this perspective to review and then challenge three oversimplifications about grassland–shrubland transitions emerging from earlier conceptual models: (1) that ongoing transitions are a simple function of livestock grazing pressure and/or drought events, (2) that shrubland states represent degradation, and (3) that grass recovery is difficult or impossible over time scales relevant to ecosystem management. We then discuss the implications of our updated transition model for sustaining, improving, and restoring the provision of ecosystem services in desert grasslands and other ecosystems.

Historical triggers and the "Jornada model" of grassland–shrubland transitions

The Jornada Basin is located in southern New Mexico, United States, within the desert grassland region of North America (figure 1). The region circumscribes areas of perennial grassland, savanna, desert scrub, and grassy shrublands or woodlands in eastern Arizona, southern New Mexico,

western Texas, and northern Mexico (McClaran and Van Devender 1995). In this region, the dominance of grasslands and shrublands or woodlands appears to have shifted 4–5 times during the Holocene (8000–10,000 BP), ostensibly in relation to major shifts in climate (Monger 2003). These pre-Anthropocene shifts are evidence that climate has played an important role in grassland–shrubland transitions at millennial timescales. Written accounts from explorers and US General Land Office survey data from the midnineteenth century indicate that warm-season (C_4) perennial grasses were dominant throughout the region, with isolated shrub-dominant communities present on shallow soils, in arroyos and river floodplains, on deep sandy soils, or where native peoples promoted certain species (e.g., *Prosopis glandulosa*, mesquite) for food and fuel (Buffington and Herbel 1965, Fredrickson et al. 2006, Peters et al. 2006). Based on the convention of recognizing vegetation present at the time of widespread Anglo-European settlement as the historical "reference state," perennial grassland is regarded as the most widespread reference ecosystem for the Jornada Basin and surrounding areas (Buffington and Herbel 1965). European settlement corresponded with a rapid increase in livestock that directly and indirectly facilitated the spread of shrubs from isolated shrubland communities.

The cattle boom of the late nineteenth century was triggered by a confluence of social, climatic, and technological factors. These factors included passage of the initial Homestead Act (1862), which enabled the acquisition of large tracts of land for ranching, the arrival of railroads that permitted cattle from the drought-stricken Great Plains to be imported to the region and that facilitated the export of beef to expanding markets, and a large influx of British and eastern US capital that supported large ranches (Sayre 1999). The coincidence of these social and ecological forces preceded modern range management and an understanding of livestock influences on ecosystems, leading to intense grazing pressure across the region. Reductions in grass cover and increased soil erosion were well documented by the early twentieth century (Grover and Musick 1990, Sayre et al. 2012) and were the impetus for creating "experimental ranges" (e.g., the Santa Rita in southern Arizona in 1903 and the JER in 1912) to provide management recommendations for desert grasslands. These initial events were followed by the expansion of native shrub species that were minor components of the desert grassland in the 1850s (Buffington and Herbel 1965). The expansion of shrubs was promoted by several concurrent mechanisms attributable to heavy grazing by livestock: reduced grass cover that alleviated competition for shallow soil water during shrub establishment, a lack of continuous fine fuels needed to carry fire that limits shrub establishment, and accelerated seed dispersal of certain shrub species (e.g., *P. glandulosa*) by cattle (Fredrickson et al. 2006, Archer et al. 2017). As shrubs proliferated across the landscape during the twentieth century, further episodes of perennial grass loss occurred in the 1930s and 1950s, when grazing impacts on grasses were magnified by drought (Yao et al. 2006, Bestelmeyer et al. 2011a), producing plant communities increasingly dominated by unpalatable shrubs. The current dominance of woody plants in the region has no precedent within the last five millennia (Brunelle et al. 2014).

Once established, shrubland states are highly persistent (i.e., the products of regime shifts) because of the longevity and vegetative regenerative capacity of woody plants and feedback loops favoring shrubs over grasses: the redistribution of soil, nutrients, and water from barren patches to patches associated with shrub canopies known as the *Jornada desertification model* (Schlesinger et al. 1990, Okin et al. 2009). Competition with shrubs for soil water, low grass-seed production, viability and longevity, and soil erosion by wind and water combine to limit grass establishment and persistence in shrub interspaces (Cox et al. 1986, Peters 2002). This has led to the widespread perception that grass loss is effectively irreversible over time frames relevant to ecosystem management (Grover and Musick 1990, D'Odorico et al. 2012).

The Jornada model of grassland–shrubland transitions articulated above is supported by a large body of research. The model emphasizes the importance of fine-scale and episodic drivers (grazing and discrete drought events) and feedback mechanisms (nutrient redistribution and reduced fire) and discrete, irreversible transitions from "healthy grassland" to "degraded shrubland" states. The model generally ignores underlying spatial heterogeneity. The literature on grassland–shrubland transitions often reflects this narrative (e.g., Asner and Heidebrecht 2005, Bestelmeyer et al. 2007, Mueller et al. 2007). We argue, however, that elements of this narrative have given rise to oversimplifications and misinterpretations that can hamper the sustainable management of desert grasslands. Furthermore, these misinterpretations limit our understanding of state changes and regime shifts more generally (Petraitis 2013).

New insights on regime shifts in desert grasslands

Below, we expand and clarify perspectives on grassland–shrubland transitions on the basis of recent data and interpretations, and we describe how this knowledge can inform management decisions and contribute to a deeper understanding of regime shifts.

Grassland–shrubland transitions are the product of multiple drivers at multiple scales. Recent research indicates that grassland–shrubland transitions are more complex than those represented in the relatively simple Jornada model described above and are caused by several triggers, drivers, and feedback mechanisms interacting across multiple spatial and temporal scales—a "new" Jornada model (figure 2). Once shrub establishment limitations were alleviated by the dual drivers of increased seed dispersal and reduced fire frequencies associated with livestock grazing, other broadscale drivers, such as aridity and atmospheric carbon dioxide enrichment, were likely able to reinforce shrub expansion (Fredrickson et al. 2006, Archer et al. 2017), representing a

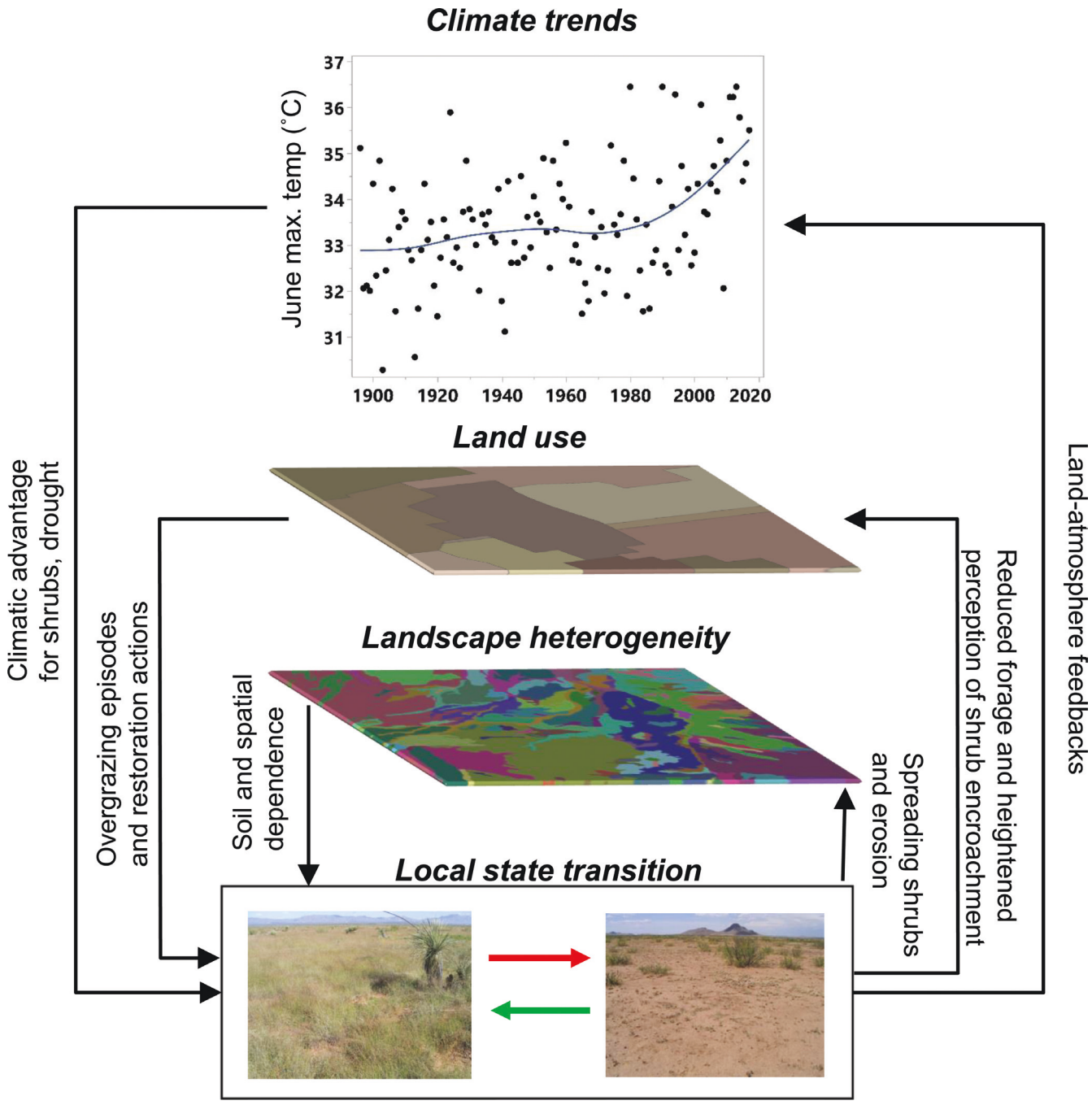

Figure 2. A conceptual model of the grassland–shrubland regime shift in the desert grassland region, highlighting the role of cross-scale feedbacks among landscape heterogeneity, land use, and climate. The top panel is the June (on average the hottest month) average daily maximum temperature (line is LOESS smoother, λ = 0.5) from New Mexico Climate Division 8, which circumscribes a large portion of the northern desert grassland area surrounding the Jornada Basin (NOAA 2017).

nearly simultaneous change in multiple controlling variables. Under current climate, shrubs physiologically outperform perennial grasses across a wide range of rainfall scenarios because shrubs can access soil water at depths inaccessible to grasses and maintain photosynthetically active leaves for longer periods than grasses (Throop et al. 2012). Climatic warming and increases in interannual rainfall variability are predicted to further promote shrubs over grasses because of the heavy reliance of grasses on ephemeral surface soil moisture (Gremer et al. 2015). Experimentally induced increases in interannual rainfall variability confirm that projected climate could favor shrub production at the expense of grass

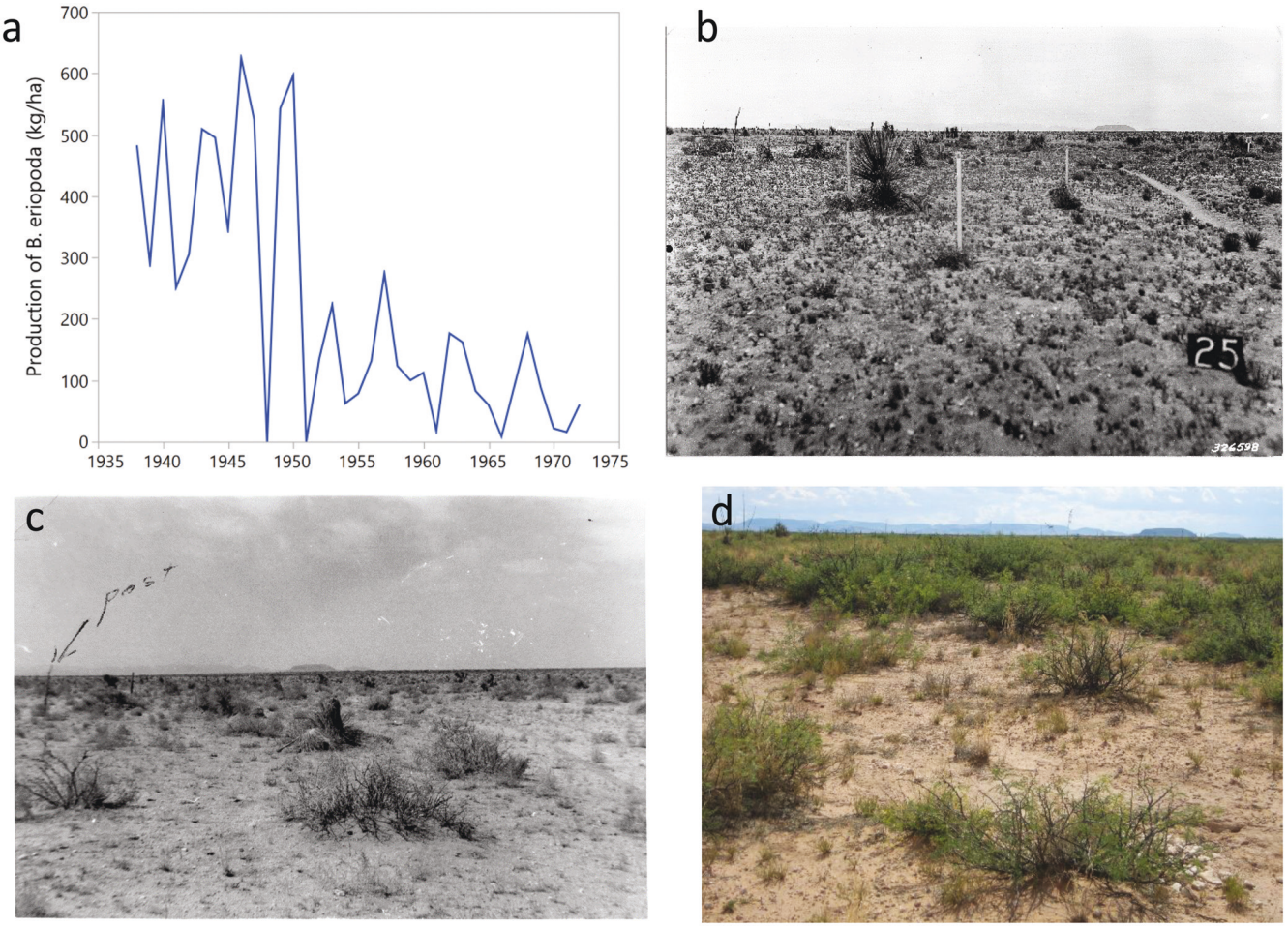

Figure 3. Evidence for the grassland–shrubland transition in the Jornada Basin: (a) The initial collapse of* Bouteloua eriopoda *(black grama) production in pasture 2 during the 1950s drought (see Bestelmeyer et al. 2011a). (b) A photograph of a site near the southern boundary of pasture 2 in 1936, illustrating the effects of overgrazing during the 1930s drought. (c) The appearance of small* Prosopis glandulosa *shrubs in 1956. (d) The site in 2009, dominated by shrubs and with evidence of significant soil erosion exposing an indurated petrocalcic soil horizon (caliche).

production (Gherardi and Sala 2015). The potential for natural or prescribed fire to slow shrub expansion where this is possible given current spatial patterns of grass productivity and fuel loads (Levi and Bestelmeyer 2016) is therefore likely to diminish. Current and projected environmental conditions toward increased aridity and variability will therefore make present-day desert grasslands increasingly vulnerable to shrub encroachment.

Climate may influence the rate of shrub encroachment, but is not necessarily the dominant driver at landscape scales because grassland–shrubland transitions are patchy and asynchronous in areas over which climate is essentially uniform. Transitions at these spatial scales are strongly mediated by the interactions of (a) local land-use regimes, (b) lateral interactions (spatial contagion), and (c) soil-geomorphic settings (Bestelmeyer et al. 2011b).

With regard to land use—and consistent with the older Jornada model—losses of dominant perennial grass cover (i.e., *Bouteloua eriopoda*, black grama) in the Jornada Basin at local scales are clearly related to discrete periods of overgrazing during drought. Such losses can be very abrupt when livestock numbers are high and are not promptly reduced following the onset of multiyear droughts, such as occurred in the 1950s (figure 3a; Yao et al. 2006, Bestelmeyer et al. 2011a). Shrub recruitment and dominance following the loss of dominant perennial grasses can take decades (figure 3b–d). In such cases, grassland states undergo an abrupt collapse followed by a gradual reorganization to a shrubland state. Patch-scale transitions occur when shrubs establish and reach a size at which they benefit from increased connectivity from wind and water, which redistributes nutrients to shrub canopies to create discrete "islands of fertility" (Schlesinger et al. 1990, Reynolds et al. 1999, Okin et al. 2009).

Once shrubland patches become large and interconnected, their expansion and replacement of perennial grasses are no longer governed by grazing pressure and become controlled

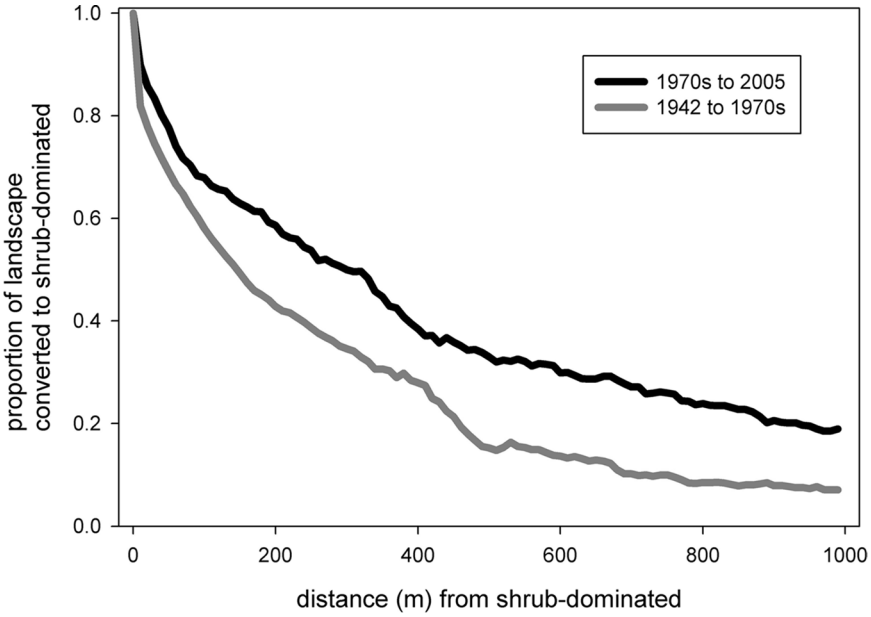

Figure 4. The proportion of a 20,000-hectare area that transitioned from grass dominated to shrub dominated at increasing distances from existing shrub-dominated areas between 1942 and the 1970s (gray line) and the 1970s to 2005 (black line). From Goolsby (2012).

instead by spatial contagion (Peters et al. 2006). Accelerating spread of dominance by *P. glandulosa* over time has been documented on sandy soils of JER (figure 4; box 1). As grass cover declines, soil eroded from areas with low vegetation cover can be deposited downwind, burying and killing grasses, reinforcing shrub dominance, and providing a mechanism for contagious transitions not directly related to grazing pressure (Alvarez et al. 2012).

Variation in soil-geomorphic setting, however, mediates the rates and patterns of shrub increase and grass loss. Notable among these are depth to restrictive barriers in the soil (e.g., indurated petrocalcic horizons) and clay content (Bestelmeyer et al. 2006a, Browning et al. 2008, 2012). Soils with high clay content or impermeable horizons near the surface diminish the advantage of deep rooting in shrubs while retaining moisture for longer periods within the rooting zone of grasses (Duniway et al. 2010), thereby mediating the rate and outcome of shrub encroachment (Archer et al. 2017).

Grassland–shrubland transitions at the landscape level involve potential feedbacks to both climate and land use (figure 2; Beltrán-Przekurat et al. 2008, Webb et al. 2017). Transition feedbacks to climate in desert grasslands are mediated by increasing dust emissions associated with shrub dominance, which also change the aerodynamic roughness of the land surface and surface energy fluxes. Increased atmospheric dust leads to surface cooling that induces subsidence and an excess of cloud condensation nuclei, both of which can inhibit precipitation, creating drier conditions that favor shrubs (D'Odorico et al. 2013, Wilson et al. 2018). In addition, increases in nighttime temperatures caused by changing surface energy fluxes might also favor shrub establishment and survival (D'Odorico et al. 2010).

Declines in forage availability accompanying increases in shrub cover can cause grazing to become more concentrated on remaining grass patches and thereby accelerate grass loss (van de Koppel et al. 2002). Alternatively, negative feedbacks to grazing pressure, such as reductions in stocking rates in response to reductions in grass production, might serve to stabilize grass cover (Yahdjian et al. 2015). Average cattle stocking rates in public (Bureau of Land Management) lands surrounding the Jornada Basin are now lower than permitted numbers and are dynamically adjusted in response to precipitation, reflecting the conservative and adaptive management strategies used by present-day ranchers (figure 5). Widespread recognition of increasing shrub dominance has also catalyzed government-led partnerships to apply selective herbicides and prescribed fire in an effort to reduce shrub cover and maintain or restore grass cover. Within the desert grassland region of New Mexico, for example, approximately 300,000 hectares have been treated with herbicides in the past 40 years to produce a mosaic of areas of high (untreated) and low (treated) shrub cover and varying grass cover (Coffman et al. 2014). These "brush management" activities have undergone a resurgence on public and private lands in the past decade (figure 6). Reduced stocking rates and increased investment in restoration represent societal feedback mechanisms opposing the loss of grasses and increases in shrubs.

Instead of abrupt transitions between discrete grassland to shrubland states, under the control of grazing and drought, the desert grassland region features a mosaic of varying grass and shrub cover structured by interacting drivers, feedback processes, and constraints operating at multiple scales. Random sampling across the Jornada Basin floor reveals that perennial grass- and shrub cover values are largely independent except at the highest shrub cover (more than 20%), at which point grass cover becomes increasingly constrained (figure 7). This independence has its origins in the spatial variation in historical grazing pressure, precipitation, soil properties, shrub contagion, and past land management. The mosaic is evolving under the direct influence of climate change, biophysical feedback mechanisms favoring shrub dominance, and societal feedback mechanisms favoring grasses (e.g., restoration activities) or shrubs (patchy overgrazing in the face of dwindling forage resources). It is to societal perceptions underpinning land use decisions that we now turn.

Shrubland states are not necessarily degraded, nor do they necessarily represent "desertification." Transitions to shrubland states

Box 1. Spatial contagion in grassland-shrubland transitions.

We evaluated contagion in grassland–shrubland transitions (i.e., the spatial spread of shrub dominance over time) using repeat aerial photography within a 20,000-hectare area of the Jornada Basin on sandy soils experiencing expansion of *Prosopis glandulosa* (figure 4). Aerial photos from 1942 and the 1970s were scanned and georectified to 2005 color digital ortho quarter-quads with a resulting common 1-meter (m) pixel resolution. For the 1970s photos, four different time periods were available (January 1973, February and November 1974, and October 1978), so only the clearest photo for each part of the study area was used. Grassland and shrub-dominated areas were then mapped to a minimum 0.5-hectare mapping unit in each time period using Feature Analyst (v. 5.0). The minimum diameter of shrub clusters that was detectable in all photos was 5 m, which is adequate to distinguish between grass and shrub dominance, even if it cannot characterize absolute shrub cover (see Laliberte et al. 2004). For each time step (1942–1970s, 1970s–2005) we calculated the proportion of the landscape that transitioned from grass-dominated to shrub-dominated in 10-m zones radiating from shrub-dominated patches present at the beginning of the time step. The proportion of the landscape transitioning to a shrub-dominated state was a decelerating function of distance from existing shrub-dominated areas, consistent with spatial contagion. Furthermore, higher proportions of the landscape transitioned to shrub dominance at greater distances from existing shrub-dominated patches between the 1970s and 2005 than between 1942 and the 1970s, indicating that contagion is accelerating, shifting from primarily infilling in the early period to more extensive spread in the later period.

have been regarded as a form of land degradation by different land users over the last century. Initially, this perception reflected the loss of forage available to livestock producers who dominate land use. More recently, shrub encroachment is associated with loss of habitat for grassland-associated biodiversity as well. Furthermore, shrubland transitions are often referred to as *desertification* because of reductions in grass productivity and accelerated soil erosion (Peters et al. 2013). Literature syntheses, however, indicate that shrub life forms may support valued ecosystem services (Eldridge et al. 2011) and that multiple objectives may be addressed by managing for mixtures of grass and woody plants (Archer and Predick 2014). Robust generalizations regarding shrub effects on ecosystem processes are hampered by the fact that "shrub" encompasses a diverse range of functional attributes and traits, such as rooting habits, longevity, and stature (Archer et al. 2017). These attributes have substantive implications for primary production, nutrient cycling, animal habitat, and land surface–atmosphere interactions. Accordingly, the impacts of shrub proliferation on ecosystem processes will depend on the traits of the shrubs involved.

One of the most striking observations from the Jornada Basin is that long-term mean annual aboveground net primary productivity (ANPP) is similar between grasslands and the shrublands that replace them (Peters et al. 2012) and across varying degrees of grass and shrub dominance on the same soil type (Schooley et al. 2018). In addition, soil carbon storage can be similar between states or be substantially greater in shrublands occupying former grasslands (Barger et al. 2011), in spite of accelerated soil erosion known to occur on certain shrubland types (Webb et al. 2014). Stability in production and soil carbon stocks can be explained by the ability of certain shrubs (e.g., *P. glandulosa*) to photosynthesize for a greater portion of the growing season than grasses because of their deep and laterally extensive root systems (Gile et al. 1997) and because these shrubs can access deep soil moisture during dry years (Throop et al. 2012).

Although plant species richness is lower in shrublands compared with the grasslands they replaced (Peters et al. 2012), shrubs can provide refugia for herbaceous species that might otherwise be eliminated in areas grazed by livestock (Welsh and Beck 1976). Shrubs can also facilitate certain grasses in desert grasslands (McClaran and Angell 2007) and arid drylands more generally (Maestre et al. 2009b). The relationship of shrub dominance to animal species and communities varies depending on the taxonomic groups and metrics in question (Fulbright et al. 2017, Stanton et al. 2018). Grassland-associated bird species with low tolerance for shrub cover, some of which are exhibiting steep regional declines in abundance (Sauer et al. 2013), may be absent in shrubland states or even areas where most shrubs have been removed in order to restore grasslands (Coffman et al. 2014). Similarly, the abundance of banner-tailed kangaroo rats (*Dipodomys spectabilis*), an ecosystem engineer in desert grasslands, declines sharply when shrub canopy cover exceeds approximately 15% (Cosentino et al. 2014). Diversity patterns in several taxonomic groups, however, indicate that shrubland states support characteristic species assemblages and shrub specialists that are not considered "weedy" or invasive, including lizards, ants, and rodents (Bestelmeyer and Wiens 2001, Cosentino et al. 2013). Furthermore, a mosaic of shrublands and grasslands may be beneficial for game species valued by the public (Saiwana et al. 1998).

Finally, historical reconstructions and photographs suggest that shrublands were present in some parts of the desert grassland region when European settlers arrived (Humphrey 1987). In some cases, these shrublands may have been associated with aboriginal human cultivation activities (Fredrickson et al. 2006); in other cases, their historical dominance reflects the fact that they are better adapted to certain soil types than grasses are (figure 8). These patches of historical shrublands are believed to have been the points of origin for the encroachment of different

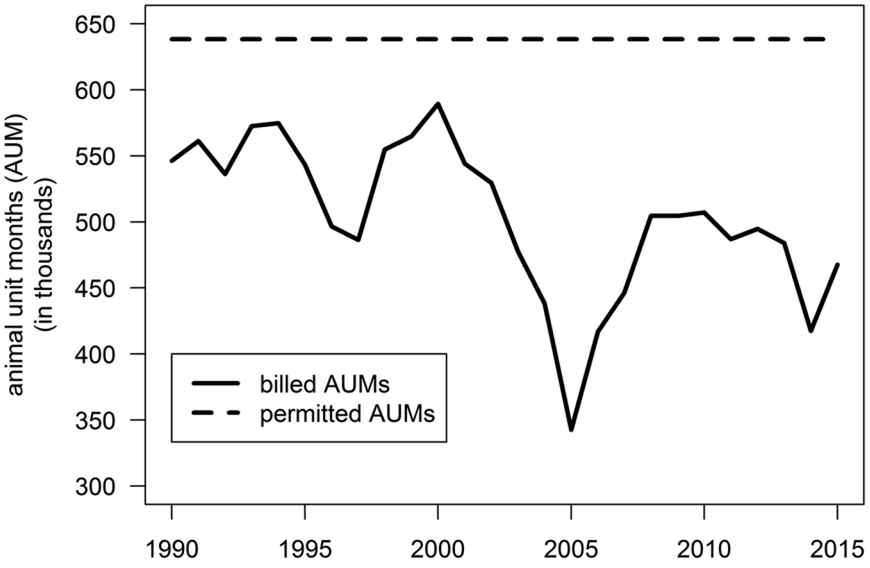

Figure 5. The management of livestock grazing on public (Bureau of Land Management; BLM) lands within the Las Cruces District, which represents approximately 2.2 million hectares of desert grassland surrounding the Jornada Basin. The dashed (top) line represents the total permitted grazing capacity (in animal unit months, AUMs: the months of grazing permitted for a 454-kilogram cow) of the district across all grazing allotments. This value reflects an estimate of carrying capacity initially determined via forage inventories after passage of the Taylor Grazing Act (1934) and only varies when permanent adjustments are made at the allotment level, which is infrequent. The solid (lower jagged) line represents the "billed" grazing capacity, which is the total number of AUMs actually purchased by ranchers in the district in a given grazing year (March–February) and is assumed to reflect actual stocking rates. Data courtesy of the BLM Las Cruces District Office.

shrub species into surrounding grasslands following changes in climate, fire, and seed dispersal regimes. Nonetheless, the existence of historical shrublands and how to distinguish them from encroached grasslands is usually not recognized by land users and management agencies (see Romme et al. 2009). Targeting these communities for shrub removal treatments with the expectation of promoting grass production may have little chance of success. An analysis of soil organic carbon stable isotopes can provide a reliable determination of whether a present-day shrubland has recently displaced a C4 grassland or whether it has been long-term constituent of the landscape (Monger et al. 2009).

With recognition of the value of shrubs and shrubland patches for songbird and game species, some land managers now consider how to manage the balance between grass and shrub life forms at different spatial scales rather than seeking to eliminate shrubs outright, as was the historical (pre-1980s) paradigm (Fulbright et al. 2017). Managers often seek to create *savannas*, grassy areas including a shrub component, even in areas where shrubs were not known to occur historically. The presence of perennial grasses between shrubs could also mitigate the most pernicious effect of shrub encroachment in arid lands, soil erosion by wind and water, if bare ground gaps are kept below a critical threshold (Webb et al. 2014). The question, then, is how to restore and sustain perennial grasses in areas where they were extirpated.

Restoration of grasslands (or at least grasses) is possible. The restoration of grassland states has had limited success over the last century in desert grassland and other arid–semiarid systems (Archer et al. 2011). Attempts to reestablish grass populations in the Jornada Basin via grazing exclusion, shrub removal, seeding, and planting have largely been regarded as failures (Herrick et al. 2006). Establishment failure is ostensibly due to a suite of physical changes in the soils and microclimate in areas between shrubs, including reduced soil aggregate stability and infiltration (Bestelmeyer et al. 2006b), elevated surface temperatures (D'Odorico et al. 2010), and increased sediment flux and abrasion of herbaceous plants (Okin et al. 2006), which vary with soil-geomorphic setting. The high likelihood of restoration failure has been extrapolated across the desert grassland region, particularly in general references to the "irreversibility" of shrubland transitions (Valone et al. 2002).

Experiences from other parts of the desert grassland region, however, have challenged this generalization. Long-term grazing exclusion (40 years) in southeastern Arizona resulted in some degree of recovery in grasses and soil properties (Allington and Valone 2011). Contrasting outcomes probably reflect spatial heterogeneity. The Arizona site features wetter climates (417 millimeters mean annual rainfall) and more fertile soils (gravelly mollisol soils in broad swales) than the Jornada Basin (232 millimeters mean annual rainfall), where livestock exclusion in coppice dune shrubland states (sandy aridisol soils on eolian plains) has often yielded no grass response. Recent studies, however, indicate that gradual recovery of the formerly dominant grass species (*B. eriopoda*) with livestock exclusion is possible on sandy aridisols if remnant grass cover exceeds 1.5% (Bestelmeyer et al. 2013).

Reductions in shrub cover instigated by land management agencies within the desert grassland region may fail to catalyze grass recovery in some cases (Brock et al. 2014) and promote it over several decades in other cases (Havstad et al. 1999, Perkins et al. 2006). However, the grass species that respond are often different from those dominating reference grassland states (Coffman et al. 2014). The cause of these inconsistent responses is poorly understood, but soil degradation is widely believed to be a primary cause of restoration

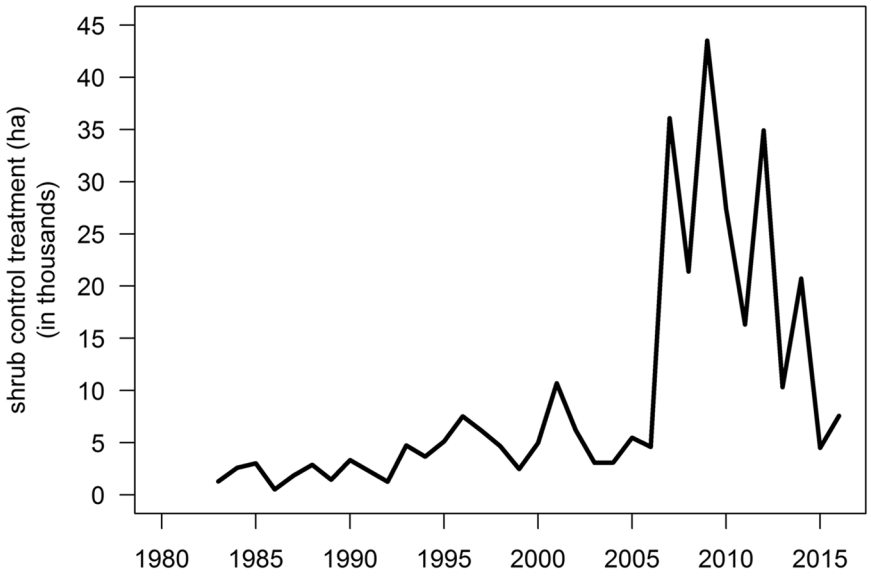

Figure 6. The area of brush management treatments per year within the Bureau of Land Management (BLM) Las Cruces District. The abrupt increase in 2007 is associated with the initiation of an interagency restoration initiative, the BLM-led Restore New Mexico program, affected by funding limitations in later years. Data courtesy of the BLM Las Cruces District Office.

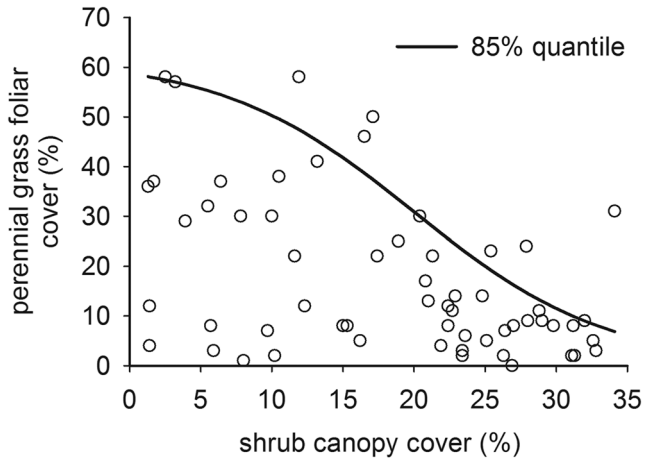

Figure 7. The relationship of perennial grass cover to shrub cover at randomly selected points within coarse-loamy soils of the Jornada Basin. The fitted line is the 85th quantile logistic curve used to visualize the increasing constraint on maximum grass cover with increasing shrub cover. From Williamson and colleagues (2012).

failures. Ongoing long-term research seeks to understand the climatic, edaphic, and management circumstances constraining the rate and extent of grass recovery.

Extreme climatic events may be required to catalyze perennial grass establishment in areas where soils are considered to be degraded (Peters et al. 2012). For example, a sequence of wet years from 2006 to 2008 on the JER led to dramatic increases in native perennial grasses to cover levels rivaling reference grasslands (approximately 30%; Peters et al. 2014). This outcome is not, however, regarded as complete restoration because the species that increased (*Sporobolus flexuosus* and other bunchgrasses) were historically subdominant and because the persistence of this flush of grasses is yet to be determined. Nonetheless, this case illustrates that grass establishment constraints associated with shrub dominance, soil erosion, and changes to soil surface properties in what are regarded as the most "degraded" of desert grassland states can be mitigated by sequences of wet years. The exploitation of cyclical or stochastic variations in rainfall is a widely recognized possibility for accelerating desired vegetation changes in drylands (Holmgren et al. 2006).

The current body of evidence suggests that gradual or abrupt recovery of perennial grasses can be achieved with a combination of interventions, including grazing and shrub management, perhaps timed to exploit sequences of high-rainfall years. Generally, restoration actions need to be carefully considered in light of the effects of landscape heterogeneity and temporal context. Full restoration, partial restoration, or even intensified desertification can occur in response to these actions. At this time, we have not organized information so that the likelihood of specific vegetation responses can be predicted for distinct parts of a landscape.

Lessons about regime shifts and their management

Studies of grassland–shrubland transitions in southwestern desert grasslands are among the longest-running, broadscale investigations of ecosystem change (more than 100 years in the case of the Jornada Basin) and reveal several insights that contribute to global perspectives on regime shifts. When viewed at the extent of landscapes (or seascapes), regime shifts can be highly heterogeneous, controlled by drivers and feedback loops occurring over a range of spatial and temporal scales (Cumming et al. 2017). Although regime shifts can be considered abrupt at centennial to millennial time scales, at the shorter (decadal) time scales of management, a shift can involve a combination of abrupt and gradual changes under the control of interacting exogenous and endogenous processes. Simplistic models based on single controlling variables and critical thresholds in equilibrium systems are therefore unlikely to yield actionable indicators for controlling regime shifts in desert grasslands and other ecosystems (Ratajczak et al. 2017).

The desert grassland case illustrates that interpreting alternative states in purely dichotomous fashion, particularly using vague, value-laden terms such as "degraded" or

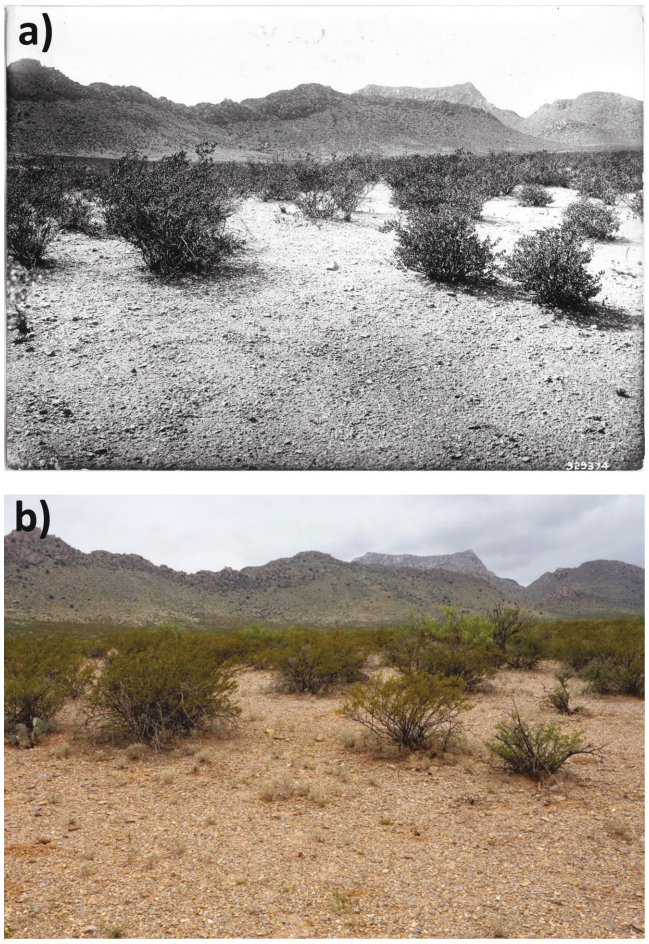

Figure 8. Repeat photographs of a site dominated by the shrub* Larrea tridentata *on the JER, (a) in 1912 taken by Elmer Wooten and (b) in 2015 taken by Patrick Alexander. Note that most of the shrubs in 1912 are still present and of similar size in 2015.

"desertified," may limit the strategies available to manage regime shifts. Although predominantly grassland and shrubland states exist and evidence for state transitions are abundantly clear, heterogeneity in the pace and outcomes of state transitions has led to a continuum of grass–shrub ratios. The functional characteristics of alternative states (including those resulting from restoration actions) may include both positive and negative effects on biodiversity and ecosystem services, and knowledge of potential trade-offs should be the basis for designing intervention strategies.

In desert grasslands, the broadscale restoration of historical grassland composition appears to be an increasingly anachronistic idea. Projected climate changes toward increased aridity and the ongoing spread of shrubs into grasslands, even where livestock grazing no longer occurs (Browning et al. 2014), suggest that in the absence of significant and repeated investment in shrub removal, shrub dominance is assured. A more realistic goal for management, then, is to consider the management of both historical and "novel ecosystems," in which the goal is to manage for specifically desired ecosystem services in parts of the landscape that are most amenable to obtaining them (Hobbs et al. 2014). This would entail management of mosaics of grassland, shrubland, and savanna states. Knowledge of the existence of historical shrublands, the soil-geomorphic contexts in which grasslands are most likely to be maintained or restored, and the ecosystem services provided in savannas can be used to prioritize the type, timing, extent and location(s) of management actions most likely to achieve a given goal. This approach requires that land management agencies and land users adopt a landscape perspective when considering the provision of ecosystem services; not all desired ecosystem services can (or should) be provided everywhere and equally in a landscape. The approach also requires knowledge systems that specify the likelihoods of ecosystem responses to management actions for different soils and ecological states in a landscape (Herrick et al. 2013).

In spite of their complexity, heterogeneous regime shifts can be managed according to a simple logic and with readily available tools. Spatial data on the estimated historical distribution of ecosystem states can be used to identify areas where restoration attempts may not be realistic (Romme et al. 2009). Spatial data on the distribution of current ecosystem states can be used to specify and prioritize monitoring and intervention activities (Steele et al. 2012, Cumming et al. 2017). These approaches should also include data on environmental contexts governing resilience, such as soil profile development in desert grasslands (Browning et al. 2012) and, similarly, shelf position in coral reefs (Cheal et al. 2013). In areas where reference states are extensive, monitoring with regard to specified limits to disturbance intensity and temporal duration (e.g., stocking rate and deferment periods), alongside the use of early warning indicators (e.g., spatiotemporal variation in grassland NPP or changes in shrub density), may be called for in environmental contexts where future resilience is in doubt (Scheffer et al. 2015, Ratajczak et al. 2017). Where reference and alternative states coexist in a mosaic, monitoring might instead be focused on the spatial spread of the alternative state.

Areas having undergone state transitions should be evaluated with the understanding that the likelihood of recovery of a reference state will be a function of local biophysical constraints to establishment, the spatial (landscape) context that governs resource and propagule flows, and our ability to manipulate these constraints and flows to promote restoration (e.g., Ludwig et al. 2007). Such evaluations can indicate where the magnitude of disturbance drivers under management control might usefully be reduced to allow recovery of historical conditions (or at least historical elements) during extreme events (Holmgren et al. 2006). In areas where the likelihood of recovering historical elements is low, interventions should instead focus on promoting processes that support specific ecosystem services, irrespective of historical fidelity (Hobbs et al. 2014).

It is also critical to recognize the feedback systems between the spatial distribution of ecological states and the human social systems that interact with them (figure 2; Qiu et al. 2018, Wilcox et al. 2018). The likelihood of change, whether it be an undesired transition or restoration, ultimately depends on the actors controlling particular areas and their motivations, their use of information, reactions to market forces, and the availability of economic resources (e.g., subsidies, cost sharing, low-interest loans, and conservation easements) that can finance management. Most regime shifts are social–ecological in nature, but social–ecological conceptualizations and the management strategies based on them continue to be rare. The development of mechanistic, social–ecological perspectives represents a primary research challenge for the next phase of regime-shift science.

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