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Long-Term Dynamics and Hotspots of Change in a Desert Grassland Plant Community

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ABSTRACT: Natural and anthropogenic disturbances are key drivers of vegetation dynamics. The hierarchical-response framework proposes that directional change in communities is driven by chronic resource alterations resulting from global environmental change in the absence of disturbance. Because vegetation is spatially heterogeneous, some local areas within a larger community may be more dynamic than others. Thus, the average rate of change may mask dynamic hotspots and local areas where vegetation remains stable. We used long-term data from two line-intercept transects in undisturbed desert grassland to quantify large-scale community dynamics, small-scale local dynamics, and boundary dynamics of grass patches in the absence of disturbance. We found that directional change in species composition was evident but that the overall rate of change varied spatially. Cover of both dominant grasses, *Bouteloua eriopoda* and *Bouteloua gracilis*, increased over the full transects, but most change occurred in localized hotspots. Patch boundaries of the dominant grasses exhibited both stability and local dynamics. Overall, the increasing abundance of *B. eriopoda* may predispose this grassland to shrub encroachment, whereas locally stable areas may prove resistant to state transition. More generally, global environmental change may be a pervasive driver of vegetation dynamics through localized hotspots of temporal change and spatially varying changes in patch boundaries in the absence of disturbance.

Keywords: plant community dynamics, Chihuahuan Desert grassland, small-scale dynamics, hotspots, boundary dynamics, time-lag analysis, *Bouteloua eriopoda*.

Introduction

In the absence of catastrophic disturbances, plant communities are assumed to occur in a quasi-steady state that represents a fluctuating equilibrium between vegetation and the environment over ecological time frames (Connell and Sousa 1983; Pickett and Cadenasso 1995; Pickett et al. 2011). Indeed, the existence of such dynamic equilibria is a fundamental assumption underlying alternative-stable-

state theory (Westoby et al. 1989; Beisner et al. 2003; Scheffer et al. 2012). Where alternative stable states are known to occur, a plant community can persist in one of several different ecological states, such as grassland or shrubland, under similar environmental conditions (D'Odorico et al. 2012). Each stable state can persist over extended time periods in the face of episodic disturbances or some degree of temporal variability in environmental drivers. In contrast, catastrophic disturbances or strong directional changes in environmental forcing can shift vegetation from one stable state to another, resulting in either a gradual or a sudden state transition, that is, from grassland to shrubland (Bestelmeyer et al. 2011). It is not clear, however, whether gradual changes in environmental conditions may lead to species reordering (changes in rank order of abundance within a community) that can ultimately destabilize ecological communities.

Within a given stable state, the scale, intensity, and frequency of disturbances create a broad suite of dynamical processes (Watt 1947; Pickett et al. 1989; Remmert 1991; Wiegand et al. 2006; Hughes et al. 2007), referred to as hierarchical patch dynamics (Wu and Loucks 1995). Under hierarchical patch dynamics, change plays out at multiple scales and over variable time frames within a long-term stable vegetation state (Bormann and Likens 1979; Remmert 1991). Hierarchical patch dynamics incorporates multiple causal agents and broadens the spatial and temporal scales within which ecological change can be meaningfully observed (Wu and Loucks 1995; Pickett et al. 2011). That is, patches within communities may differ in their rate of change over time and in the mechanisms that drive change.

Under a patch-dynamics framework, patches within a larger mosaic are defined as relatively discrete areas that differ in biotic and/or abiotic structure and composition from their immediate surrounding state (Pickett and Cadenasso 1995). Because patches are discrete, they must also have an edge or boundary that separates them from

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adjacent patches. Indeed, boundaries or edges (and, to some extent, ecotones—the gradual transition from one ecological community to another) are often defined as multidimensional zones that delimit patches (Cadenasso et al. 2003a, 2003b). Studies on ecological boundaries, however, have been primarily concerned with their delimitation and functioning, more so than with their spatial dynamics (Gosz 1993; Fagan et al. 2003; Cadenasso et al. 2003b). With the exception of alpine tree lines (e.g., Tinner and Theurillat 2003) or tree-grass interactions in savanna (Jeltsch et al. 2000; Wiegand et al. 2006), less attention has been paid to the dynamics of boundaries themselves. Moreover, in spatial ecology, most boundaries are treated as fixed, which may constrain our understanding of vegetation dynamics as patches expand and contract over time (Peters et al. 2006a).

Peters et al. (2006a) recognized that vegetation is inherently patchy and that patch boundaries themselves could be spatially dynamic, creating a potent mechanism for change in species composition over time in the absence of disturbance. Yet boundary dynamics has received little attention relative to turnover in species composition within stationary patches. Moreover, it is likely that rates of patch dynamics within communities are highly variable (e.g., Bestelmeyer et al. 2006a, 2006b; Duniway et al. 2010), creating “hotspots” and “cold spots” of community change analogous to biogeochemical hotspots and cold spots at the interface of terrestrial and aquatic systems (McClain et al. 2003). Such hotspots of change may lead to instabilities that can trigger state change, such as grassland-to-shrubland transitions (Wiegand et al. 2006), whereas cold spots may provide resistance to state transitions by providing local refugia where species and communities persist over time (e.g., Randin et al. 2009).

Chronic resource alterations as a product of global environmental change (e.g., increased atmospheric nitrogen deposition, warming, elevated atmospheric CO₂ concentrations, and increased precipitation variability) can produce vegetation change in the absence of natural or anthropogenic disturbances (Clark and Tilman 2008; Collins et al. 2008a; Smith et al. 2009). Some ecosystems, especially herbaceous-dominated communities, are highly responsive to interannual variation and directional change in resource availability and disturbance regimes (Knapp and Smith 2001; Stevens et al. 2004; Suding et al. 2005; Cleland et al. 2013; Isbell et al. 2013). Aridland ecosystems, in particular, are predicted to be exceptionally responsive to anthropogenic change (Diffenbaugh et al. 2008). Indeed, because of their strong sensitivity to environmental variability (Heisler-White et al. 2008; Thomey et al. 2011; Maestre et al. 2012) and relatively discrete patch structure (Schlesinger et al. 1996; Kröel-Dulay et al. 2004), aridland

communities are ideal systems for quantifying the spatial and temporal complexities of vegetation dynamics.

In this study, we analyzed two unique 20-year-long data sets from an undisturbed desert grassland plant community in the northern Chihuahuan Desert to quantify large-scale community dynamics, localized small-scale dynamics, and the dynamics of dominant species in the absence of large-scale disturbances, such as fire and grazing. We addressed the following questions regarding spatial and temporal change: (1) Is this desert grassland undergoing directional change in the absence of disturbance, or does this community simply fluctuate in response to interannual climate variability? (2) Are there local hotspots and cold spots of community change over time, or is rate of change more or less uniform spatially? (3) Do the patch boundaries of the dominant grasses remain stable, or do they fluctuate or expand directionally over time? By answering these questions, we can determine whether community change over time is a function of both localized hotspots of temporal variability and spatially dynamic changes in patch boundaries.

Methods

Study Site

This study was conducted from 1989 through 2008 at the Sevilleta National Wildlife Refuge (SNWR; latitude 34°20'N, longitude 106°43'W), Socorro County, New Mexico. Before its designation as a wildlife refuge in 1973, the area had been grazed extensively for decades. However, cover of the dominant grass, *Bouteloua eriopoda* (black grama), inside grazing exclosures on a neighboring cattle ranch was comparable to cover of ungrazed vegetation on the SNWR after 13 years (fig. A1; figs. A1–A4 available online). Thus, grassland vegetation on the SNWR likely had recovered extensively from grazing by 1989, when our study was initiated.

Two common grassland communities occur in the SNWR, separated by a broad ecotone: desert grassland dominated by *B. eriopoda* and shortgrass steppe dominated by *Bouteloua gracilis* (blue grama; Hochstrasser et al. 2002). *Bouteloua eriopoda* is a shallow-rooted perennial C₄ species that spreads primarily via stolons and occasionally by seed reproduction (Fields et al. 1999; Peters and Yao 2012). Individual clones live for up to 40 years (Gibbens and Lenz 2001). Its congener, *B. gracilis*, is also shallow rooted, but this perennial C₄ bunchgrass may live for centuries (Gibbens and Lenz 2001). Seedlings are rare, such that this species spreads solely by basal tillering, often forming rings (Coffin and Lauenroth 1991; Ravi et al. 2008).

Overall, these two grasses account for more than 80% of the total plant cover across this ecotone (fig. A2), and

they control the abundances of subdominant species (Peters and Yao 2012). Other common species include scattered shrubs or subshrubs (e.g., *Yucca elata* and *Ephedra torreyana*) as well as a mix of other grasses and forbs (e.g., *Pleuraphis jamesii*, *Sporobolus* sp., *Melampodium leucanthum*, and *Sphaeralcea* spp.; Muldavin et al. 2008). Bare soil accounts for 25%–40% cover in this ecosystem. Soils were classified as sandy loams with approximately 68% sand, 22% silt, and 10% clay (Keift et al. 1998). Water-holding capacity and nutrient reserves of these soils are very low (Zak et al. 1994), and soils are highly erodible when vegetation cover and organic residues are removed, such as after a fire (Ravi et al. 2007) or shrub encroachment (Turnbull et al. 2010a, 2010b).

Precipitation, temperature, and soil moisture data from the winter of 1989 through 2008 were recorded daily at a climate station at Deep Well maintained by the Sevilleta Long-Term Ecological Research Program. This climate station is located about 1–2 km north of our two study sites. Average annual precipitation in the area was ~250 mm, more than half (~140 mm) of which occurred during the summer monsoon, which can extend from late June through early September (Pennington and Collins 2007; Notaro et al. 2010). The remaining precipitation comes as a mixture of snow and rain during winter and spring. Thunderstorms during the monsoon season provide intense but highly localized rainfall (Gosz et al. 1995; Pockman and Small 2010; Petrie et al. 2014), and monthly and daily rainfall extremes typically occur during this period. Although highly variable, there was no general trend in annual or monsoon precipitation during the 20 years of this study (fig. A3) or over the past 100 years (Petrie et al. 2014). Average annual temperature is 13.2°C (average daily temperature is 1.6°C in January and 25.1°C in July), but the region has experienced a strong increase in mean annual temperature, resulting in increasing aridity (Gutzler 2013). Mean daily maximum/minimum temperatures varied from 34°/14°C in summer to 10°/–7°C in winter.

Vegetation Sampling

Permanent quadrats provide a powerful tool to measure and quantify vegetation dynamics, but fixed quadrats are often too small or too few to detect changes in patch boundaries. To address this deficiency, data for this study were collected in May and September each year from 1989 to 2008 along two permanently located 400-m-long line-intercept transects (Collins 2013). Each transect (Deep Well [DW] and Five Points [FP]) was oriented north-south, with the end of the DW transect located approximately 0.5 km north of the start of the FP transect. A lightning-caused wildfire burned all of the DW transect and sections of the FP transect in August 2009; thus, we

limited our analyses to data recorded from 1989 through 2008.

To sample vegetation cover, a 100-m measuring tape was affixed to the 0-m rebar stake (north end of each transect) and run south to the 100-m transect marker. To minimize year-to-year variation in transect location, the tape was attached to permanent pieces of rebar hammered into the ground along the 100-m segment and stretched as tightly as possible to get the straightest line. Sampling on windy days was avoided. Each species or substrate (e.g., litter, bare soil, lichen, rock) encountered along the line was recorded at 1-cm resolution, noting the place the species/substrate first crossed the tape. Plant fragments smaller than 1 cm were assigned a cover interval of 1 cm. The ending point was considered to be the starting point of the next species/substrate. Thus, there are no gaps in the data stream along each transect. This procedure was then repeated for each of the other three 100-m-long segments along each 400-m sampling transect.

Data Analysis

We used start-stop distances by species to determine total cover for each species along each transect in each year. We used the maximum cover value (May or September) recorded for each species along each transect in each year for all analyses of cover, grass patch boundaries, and community dynamics. We analyzed rates of community change at two scales, using total cover for each species along the full 400-m length of each transect and species cover values in a total of 40 contiguous, nonoverlapping 10-m segments of each transect in order to determine whether local hot-spots of community change occurred over time. Although somewhat arbitrary, evenly sized segments are required to calculate comparable rates of change over time. We selected 10-m segments as the minimum length necessary to accurately measure community composition as well as to minimize any potential effects of year-to-year variation in placement of the meter tape.

We used time-lag analysis (Collins 2000; Collins et al. 2000) to quantify the rate of change in community composition over time on the basis of species abundances (cover). To do so, we calculated a Euclidean distance (ED) resemblance matrix from a species cover \times year data matrix as follows:

$$ED = \sqrt{\sum_{i=1}^S (x_{ij} - x_{ik})^2},$$

where x_{ij} is the abundance of the i th species in the j th time period, x_{ik} is the abundance of the i th species in the k th time period, and S is the total number of species. Next, we plotted the ED values at each time lag from 1 to n time lags (years). By using all time lags, the analysis pro-

duced a measure of global stability or change and reduced the influence of an unusual starting year (Collins et al. 2000). In this case, sampling from 1989 through 2008 yielded 20 sample points in time, with 19 1-year ED time lags (1989 vs. 1990, 1990 vs. 1991, ..., 2007 vs. 2008), 18 2-year ED time lags (1989 vs. 1991, 1990 vs. 1992, etc.), and so on, through one 19-year ED time lag (1989 vs. 2008), for a total of 190 time lags over the entire period. We then calculated a linear regression of time lag (independent variable) versus ED (dependent variable) for each time series (Collins et al. 2000). This analysis was then followed by time-lag analyses for each 10-m segment of each transect, to determine whether local hotspots or cold spots occur in the rate of community change over time.

Time-lag analysis can produce several patterns with time-series data. If the regression line is significant, positive, and linear, then it implies that the community is undergoing directional change (Collins 2000). If the regression line is not significant or the slope is not significantly different from 0, it indicates that the community exhibits stochastic variation over time but lacks directional change. The regression coefficient is a measure of signal versus noise. For example, a significant positive relationship with a shallow slope and a weak r^2 value suggests that directional change is occurring but that change is slow and stochastic variation is high. A higher r^2 value and a steeper slope would indicate a stronger signal of directional change and less noise.

Perennial grasses can increase in abundance via two quantifiable mechanisms, an increase in the number of "individuals" (by reproducing clonally or via seed reproduction) and an increase in the average size of existing individuals. In this case, an individual is a segment of line intercept covering a species. Obviously, the line-intercept transect could intersect the edge or center of an individual grass clone, but averaging over hundreds of individuals along each transect minimizes this bias. We quantified the number of occurrences of "individuals" and average clone size for the two dominant grasses, *B. eriopoda* and *B. gracilis*, across the full 400-m transect. We used linear regression to determine whether the abundance of the dominant species, the average size of dominants, or the number of individual clones changed over time.

Given that *B. eriopoda* and *B. gracilis* account for the majority of vegetation cover and biomass in this desert grassland, areas with high abundance of these species are generally considered to be patches (Peters 2002). Many patches of the two species overlap, whereas some are monospecific. Edges can be defined as areas where larger patches that include multiple individuals of *B. eriopoda* and *B. gracilis* start and stop. To determine whether the patch boundaries of *B. eriopoda* and *B. gracilis* were stationary or dynamic over time, we plotted the spatial-tem-

poral distribution of grass patches along each transect formed by these two widespread, dominant species and looked for changes in patch boundaries over time.

Results

A total of 76 and 77 species occurred in the DW and FP transects, respectively, during the 20-year study period. Both transects were dominated by the Chihuahuan Desert grass *Bouteloua eriopoda*, but the DW transect also included relatively high cover of the shortgrass steppe species *Bouteloua gracilis*. A number of other C_4 grasses occurred at both sites, including *Sporobolus cryptandrus*, *Sporobolus flexuosus*, *Pleuraphis jamesii*, *Aristida purpurea*, and *Muhlenbergia arenicola*. Common forbs included the subshrub *Gutierrezia sarothrae* and the perennial forbs *Machaeranthera pinnatifida* and *Sphaeralcea polychroma*.

Vegetation along both transects was undergoing directional change from 1989 through 2008, but the overall rate of change (slope of the time-lag regression) differed significantly between DW and FP, according to a t -test (DW slope = 2.90; FW slope = 0.53; $z = 8.26$, $P < .01$; fig. 1). In general, vegetation along the FP transect, which had much higher and continuous dominance by *B. eriopoda*, exhibited a rate of change much lower than that along the more northern DW transect, where *B. gracilis* was more abundant. At FP, this directional change reflects an overall increase in the abundance of *B. eriopoda* but little change in cover by the shortgrass steppe species *B. gracilis* (fig. 2). Indeed, cover of *B. eriopoda* increased from 25% (110 m out of a possible 400 m) in 1989 to around 36% (145 m out of 400 m) by 2008, whereas cover of *B. gracilis* increased a total of only 3 m, or from 6% to 7%, during this time span (fig. 2). At DW, cover of both *B. eriopoda* and *B. gracilis* significantly increased over time (fig. 2). Cover of *B. eriopoda* doubled from 14% to 29%, while cover of *B. gracilis* increased from 8% to 14% over this 20-year period. Rate of change in each 10-m segment was positively correlated with change in cover of *B. eriopoda* in each segment from 1989 through 2008 at both DW ($r^2 = 0.32$, $P < .01$) and FP ($r^2 = 0.51$, $P < .0001$). The time-lag slopes were not correlated with change in cover of *B. gracilis* or with starting cover of either species along either transect. Thus, large-scale vegetation change, as reflected primarily in higher cover of the dominant C_4 grass *B. eriopoda*, occurred along both transects but at different rates in the absence of disturbance in this native desert grassland.

Not only did community dynamics vary between the two transects, but the rate of change also varied among segments of each transect, reflecting hotspots and cold spots of vegetation dynamics, particularly at DW (fig. 3). Indeed, along several 10-m segments of the DW transect, cover of *B. eriopoda* increased by nearly 4 m over 20 years, and in one

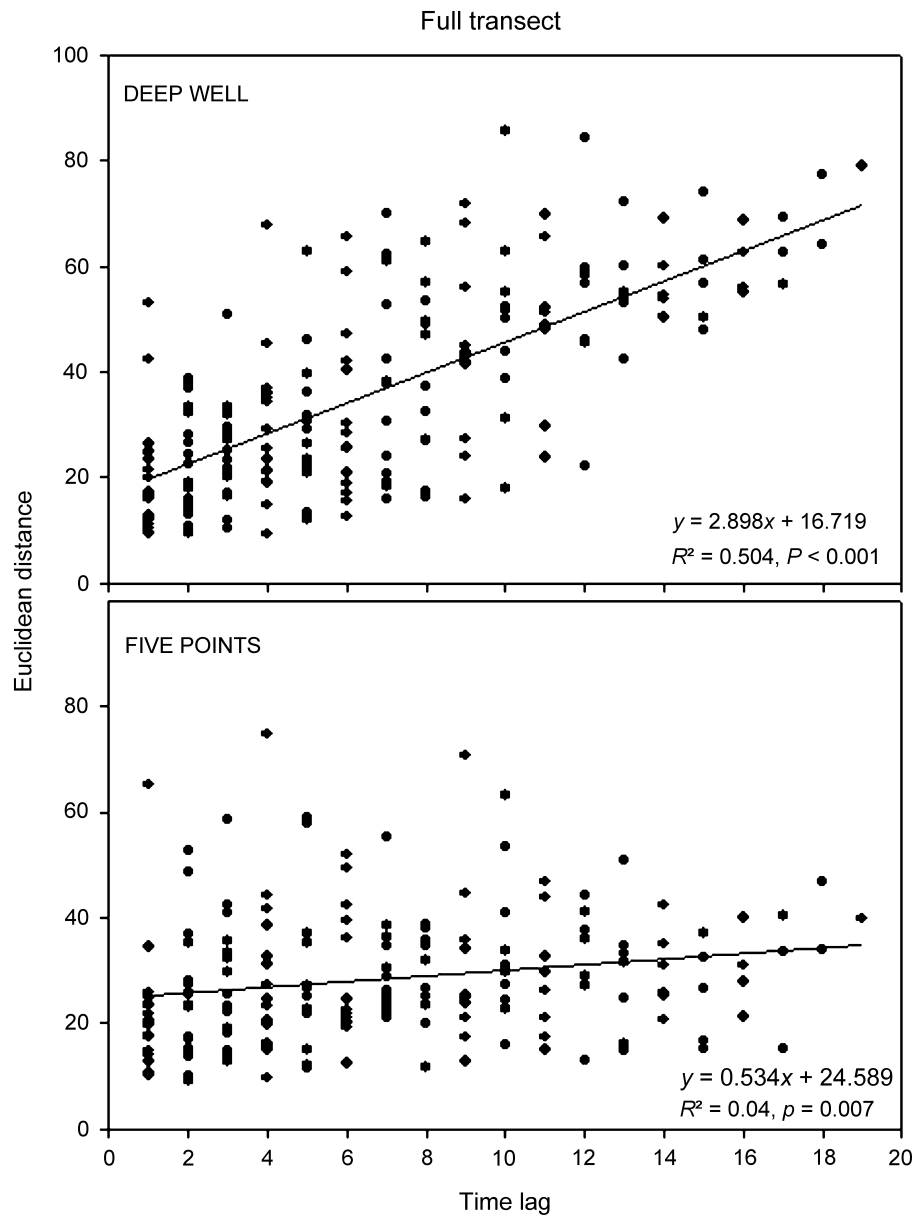


Figure 1: Time-lag analysis of change in community composition from 1989 to 2008 along two 400-m line-intercept transects in undisturbed Chihuahuan Desert grassland in central New Mexico. In both cases, the slopes were positive and significant, indicating directional change. However, rate of change was greater (steeper slope) at the Deep Well transect, where both *Bouteloua eriopoda* and *Bouteloua gracilis* were common, than at the Five Points transect, which was primarily dominated by *B. eriopoda*.

segment *B. eriopoda* cover increased by more than 6 m. This rate of change is also reflected in the slopes of the time-lag regressions of community dynamics occurring along each 10-m segment. The time-lag analysis is based on all species that occurred in a given segment of the transect, not just the dominant grasses. At DW, slopes ranged from 0 (no change) to 0.15 (rapid change), and in some cases adjacent 10-m segments differed dramatically in their rate of change.

At FP, *B. gracilis* increased in some segments by about 1 m, but this species exhibited little change along a large portion of the middle of the transect. Nevertheless, time-lag analysis again revealed variable rates of change from one segment to the next at FP (fig. 3).

At DW, both the number of individuals and the average size of each individual of *B. eriopoda* increased significantly over time (fig. 4). In contrast, the average size of individual

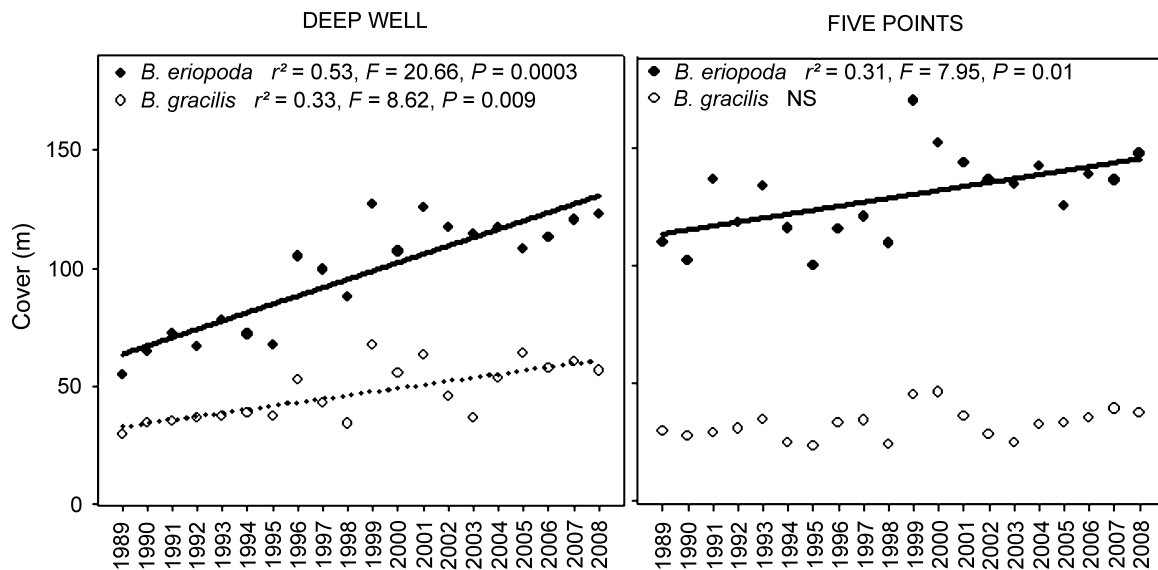


Figure 2: Change in total cover of *Bouteloua eriopoda* and *Bouteloua gracilis* from 1989 to 2008 along two 400-m line-intercept transects in undisturbed Chihuahuan Desert grassland in central New Mexico. In both cases, cover of *B. eriopoda* increased more than did cover of *B. gracilis*.

B. gracilis plants remained constant, whereas the number of individuals increased over time. No significant changes in average size or number of individuals occurred for *B. eriopoda* or *B. gracilis* along the more southern FP transect (data not shown). Thus, at DW, where strong directional change was occurring in the absence of disturbance, total cover of *B. eriopoda* increased along the transect by nearly 70 m (i.e., a rate of $>3 \text{ m year}^{-1}$) because of an increase in the number of individuals from around 350 to 500 as well as an increase in the average size of those individuals (from around 15 to 25 cm). In contrast, cover of *B. gracilis* increased by about 20 m only because of an increase in the number of individuals from 220 in 1989 to just under 400 by 2008.

The DW transect provides examples of patches of dominant grasses that have either stationary, directional, or shifting boundaries (fig. 5). Patches of both *B. eriopoda* and *B. gracilis* exhibited relatively discrete stationary boundaries throughout the 20-year study. However, patch boundaries of *B. eriopoda* also showed directional change along one end of the transect, where this species was originally absent but has increased by around 2 m on average over the last 30 m of the transect (fig. 3). At two intervals along the transect (25–50 and 320–370 m), the patch boundaries of *B. eriopoda* have shifted over time, resulting in little net overall change. Thus, evidence for all three temporal patterns of patch boundaries (stationary, shifting, and directional) exists along these two transects over this 20-year time period.

Discussion

From 1989 to 2008, this visually homogeneous grassland underwent directional change in species composition, but at the whole-community scale the rate of change varied, depending on the degree of dominance by the Chihuahuan Desert grass *Bouteloua eriopoda*. Where *B. eriopoda* was initially abundant (FP), less overall change occurred. Where the community was originally a mixture of *B. eriopoda* and *Bouteloua gracilis* (DW), much greater change occurred over time, because both species increased in overall abundance. These large-scale changes, however, masked dramatically variable rates of change at the local scale. In some cases, these changes reflected rapid expansion, or hotspots of change, within a fixed area, as might be expected under a traditional patch-dynamics model. In other cases, however, dynamics occurred because patch boundaries of both dominant grasses expanded and shifted directionally. As a consequence, overall directional change in this undisturbed desert grassland can be viewed as a multidimensional process, in which segments change in composition over time within fixed areas and in other places the boundaries of dominant grass patches themselves move, expand, and contract over time.

The dynamical hotspots observed in our study were primarily the consequence of changes in the abundance of the Chihuahuan Desert grass *B. eriopoda*. Overall, these desert grassland soils are very low in nutrients and organic matter (Zak et al. 1994). However, the two dominant pe-

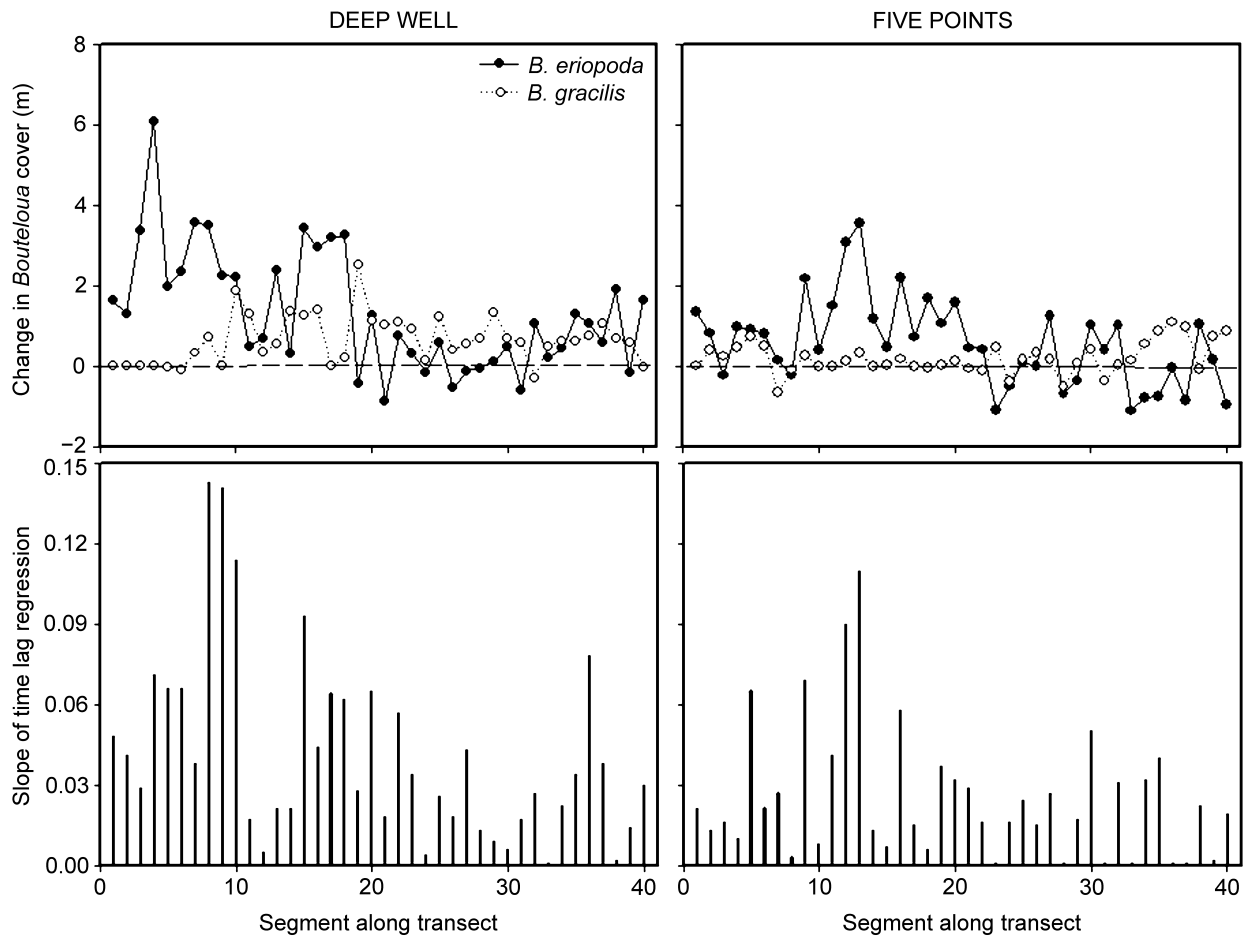


Figure 3: *Top*, change in cover of *Bouteloua eriopoda* and *Bouteloua gracilis* from 1989 to 2008 within 10-m segments of two 400-m-long line-intercept transects. Change was calculated as the difference between the average cover of each species from 1989 to 1991 and average cover of each species from 2006 to 2008. The 3-year window was used to minimize the impact of extreme years on overall change. *Bottom*, time-lag analysis of each 10-m segment of the Deep Well (left) and Five Points (right) 400-m line-intercept transects. The higher the slope, the greater the overall rate of community change over time. Both “hotspots” and “cold spots” of change occurred over 20 years along each transect.

rennial grasses are distributed across a gradient of soil texture, with *B. eriopoda* occurring on coarser-textured soils and *B. gracilis* found on finer-textured substrates (Kröel-Dulay et al. 2004). Thus, one of the potential mechanisms leading to dynamical hotspots and cold spots could be variability in soil texture underlying different patches of *B. gracilis* and *B. eriopoda*.

At the transect scale, there is a strong positive correlation between changes in total cover of *B. eriopoda* and *B. gracilis* from one year to the next (FP: $r^2 = 0.764$, $P < .0001$; DW: $r^2 = 0.837$, $P < .0001$; fig. A4), in association with interannual variation in summer precipitation. At the patch scale, no correlation was found between percent changes of *B. eriopoda* and *B. gracilis* along the 10-m segments of each transect (FP: $r = -0.137$, $P = .40$; DW:

$r = 0.24$, $P = .14$). A negative correlation might be expected if one species was displacing the other. Thus, interspecific competition between *B. eriopoda* and *B. gracilis* is unlikely to be the main driver of change in this desert grassland. Instead, change in the abundances of these species is likely occurring in response to directional changes in multiple environmental drivers. For example, Collins et al. (2010) found that cover of *B. eriopoda* increased with nighttime warming, whereas cover of *B. gracilis* increased under low rates of N deposition (2 g m^{-2}). These environmental drivers likely interact with the differential ability of these grasses to spread clonally and by seed reproduction, processes that are constrained by gradients in soil texture and patterns of seasonal precipitation (Peters 2002; Kröel-Dulay et al. 2004).

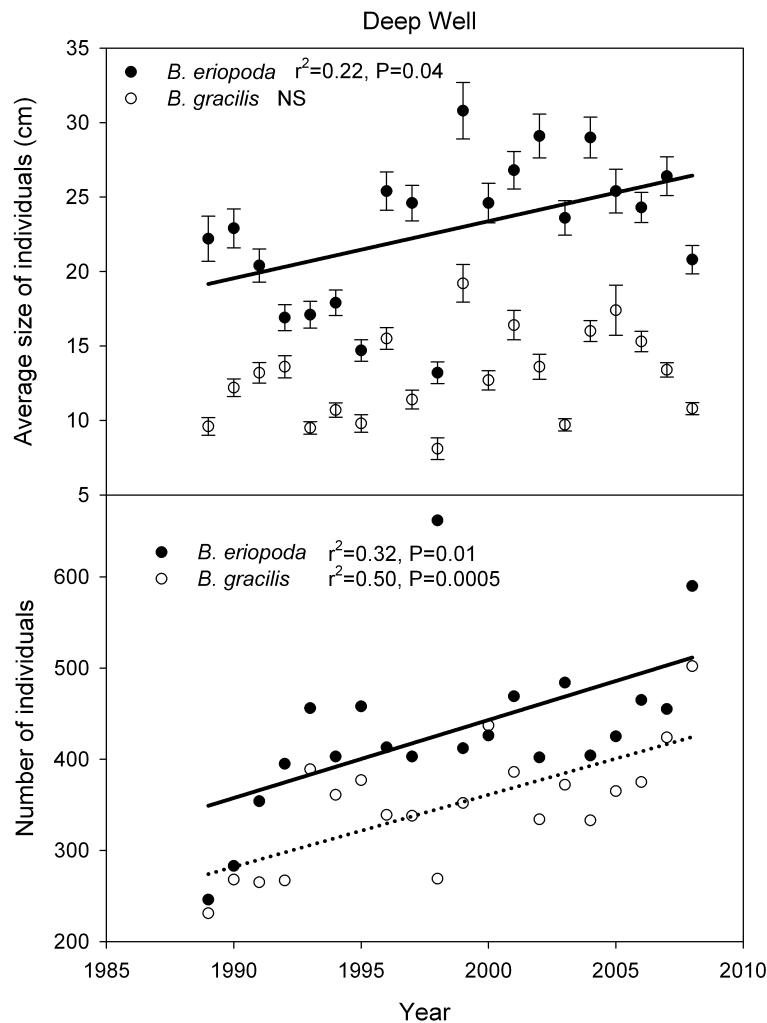


Figure 4: Change in size (*top*) and number of individuals (*bottom*) of *Bouteloua eriopoda* and *Bouteloua gracilis* along the 400-m Deep Well transect. The number of individuals of each species increased significantly over time, but only individuals of the stoloniferous *B. eriopoda* also increased in average size over time. Error bars represent ± 1 standard error.

Despite these convergent responses to interannual precipitation, *B. eriopoda* and *B. gracilis* differ in response to directional changes in several key environmental drivers. *Bouteloua gracilis* is more drought, grazing, and fire tolerant than *B. eriopoda* (Gosz and Gosz 1996; Báez et al. 2013; Ladwig et al. 2014). Moreover, *B. gracilis* appears to be a superior competitor to *B. eriopoda*. Using a long-term removal experiment, Peters and Yao (2012) found that when *B. gracilis* was removed *B. eriopoda* occupied that space through clonal growth and new seedlings but that the reverse did not happen. In addition, *B. eriopoda*, but not *B. gracilis*, responded rapidly and positively to experimental nighttime warming, which has been occurring at this site over the past century (Collins et al. 2010). In contrast, *B. gracilis*, but not *B. eriopoda*, responded posi-

tively to the addition of as little as $2 \text{ g N m}^{-2} \text{ year}^{-1}$ (Báez et al. 2007; Collins et al. 2010), although cover of both species increased after 15 years of high rates of N addition (10 g N m^{-2} ; Ladwig et al. 2012). Atmospheric nitrogen deposition is also increasing at the SNWR and regionally (Fenn et al. 2003; Báez et al. 2007). Furthermore, Thomey et al. (2014) found that rates of leaf-level carbon fixation were higher in *B. gracilis* than in *B. eriopoda* after rainfall pulses under two different experimental precipitation regimes in plots where they co-occurred. Thus, by nearly all measures *B. gracilis* should be replacing *B. eriopoda* in this grassland, but the opposite is occurring (fig. 2).

The strong increase in the Chihuahuan Desert grass *B. eriopoda*, relative to the shortgrass steppe species *B. gracilis*, would be expected under increasing aridity, which is al-

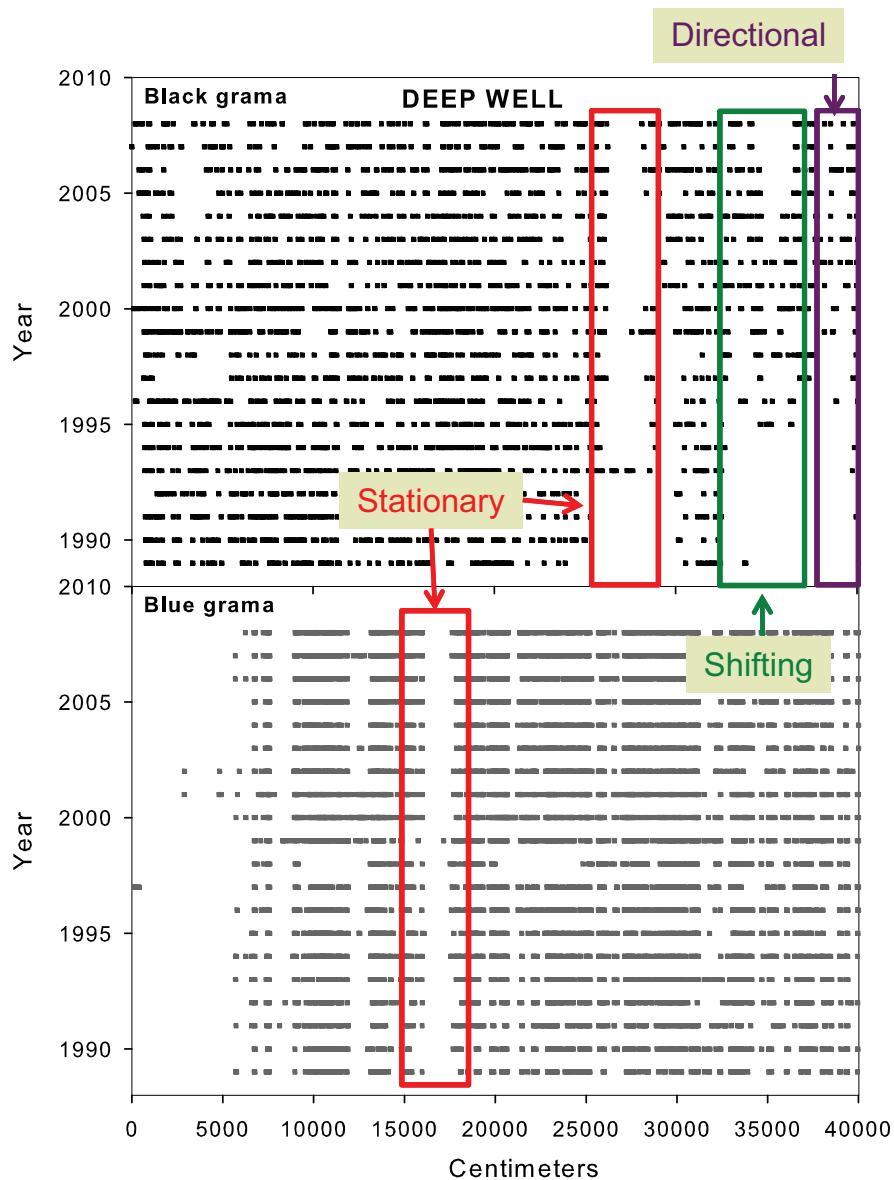


Figure 5: Changes in boundaries of *Bouteloua eriopoda* (black grama) and *Bouteloua gracilis* (blue grama) patches along the 400-m Deep Well transect from 1989 to 2008. All start and stop cover intervals of *B. eriopoda* and *B. gracilis* are plotted for each year. Three types of boundary dynamics occurred. Some boundaries were stationary, and some changed directionally through patch expansion, while others shifted back and forth over 20 years, resulting in no net change in patch boundary location.

ready occurring in this region as an outcome of climate change (Seager et al. 2007; Gutzler and Robbins 2011). As noted above, *B. eriopoda* spreads primarily via stolons and occasionally by seed reproduction (Fields et al. 1999; Peters and Yao 2012), whereas its congener *B. gracilis* spreads solely by basal tillering, which results in rings that expand slowly and eventually fragment (Coffin and Lauenroth 1991; Ravi et al. 2008). These two patterns of clonal growth explain how cover of *B. eriopoda* can increase as more

individuals are established via seedlings and tillering and those individuals increase in size, whereas cover of *B. gracilis* increases slowly and only through production of new individuals via ring expansion and fragmentation (fig. 4).

Changes in the abundances of *B. eriopoda* and *B. gracilis* are consistent with the dynamic-patch-boundary model of Peters et al. (2006a), which proposes that ecological boundaries are themselves dynamic, potentially leading to large-scale change in plant community composition. Cur-

rently, grassland ecosystems are changing globally as native C_3 trees and shrubs invade C_4 -dominated grasslands (Van Auken 2000; Sankaran et al. 2005; Wiegand et al. 2006; Knapp et al. 2008; Eldridge et al. 2011), resulting in alternative stable states (D'Odorico et al. 2012). This phenomenon is well documented in the central and southwestern United States as a consequence of multiple causes, including overgrazing, fire suppression, drought, climate variability, elevated atmospheric CO_2 , and land use change (Archer 1989; Van Auken 2000; Bond and Midgley 2012). Consequences include regional changes in net primary production and carbon sequestration (Jackson et al. 2004; Knapp et al. 2008), loss of biodiversity (Báez and Collins 2008; Ratajczak et al. 2012), increased erosion (Turnbull et al. 2010a, 2010b), and ultimately land degradation and desertification (Reynolds et al. 2007; Kefi et al. 2007). In central New Mexico, encroachment by the native C_3 shrub *Larrea tridentata* (creosote bush) occurs only in patches dominated by *B. eriopoda* (Peters and Yao 2012) because the crown morphology and high surface-root density of *B. gracilis* limit establishment of *L. tridentata* seedlings (Peters et al. 2006b). Thus, although current dynamics results in this grassland remaining as grassland, the increase in *B. eriopoda* observed here could destabilize the system by paving the way for a state change to *Larrea*-dominated shrubland.

Empirical evidence at multiple scales supports the concept of dynamical hotspots and cold spots in other types of plant communities. For example, using a regional climate model, Higgins and Scheiter (2012) noted that shifts from grassland to savanna and from savanna to forest across Africa occurred at various rates and at different times in history. On a local scale, Czaran and Bartha (1992) found highly variable rates of change in adjacent permanent quadrats within a successional old field in New Jersey. Finally, alpine tundra plant communities exhibited high local compositional change but overall global stability in the face of directional environmental change (Spasojevic et al. 2013). Together, these studies provide empirical support for the hierarchical nature of dynamic processes and rates of change that vary spatially and temporally in different types of plant communities.

Although natural disturbances remain as one of the fundamental drivers of change in ecological communities (Pickett and White 1985; Hughes et al. 2007), it is clear that mechanisms other than disturbance, such as nutrient addition, can induce relatively rapid spatial and temporal vegetation dynamics. To this end, Smith et al. (2009) proposed the hierarchical-response framework (HRF), which predicts that community dynamics now and in the future will be driven by chronic resource alterations (e.g., increased atmospheric nitrogen deposition, elevated atmospheric CO_2 concentrations, warming, increased precipi-

tation variability) due to anthropogenic environmental change in the absence of natural or anthropogenic disturbances.

Rapid and persistent dynamics in late-successional vegetation is not restricted to desert grassland communities. Collins et al. (2012) found that long-term irrigation during the growing season resulted in nonlinear responses and altered community structure in an ungrazed lowland tall-grass prairie in Kansas. Runkle (2013) documented a dramatic decrease in beech (*Fagus grandifolia*) and an increase in sugar maple (*Acer saccharum*) over 32 years in an old-growth hardwood forest in Ohio. The abundance of more than half of the tropical tree species at Barro Colorado Island, Panama, has changed by more than 25% in 28 years, including a large proportion of species that have changed by more than 50% (Hubbell 2008). Indeed, some have hypothesized that the projected directional changes in climate will lead to no-analog communities, in the absence of disturbance, by the end of this century (Williams and Jackson 2007). Thus, surprisingly rapid change in abundance and composition in communities dominated by long-lived species may now be the norm in many mature, undisturbed plant communities.

Aridland ecosystems are known to be highly responsive to anthropogenic change (Van Auken 2000; Reynolds et al. 2007). The dynamics of water-limited ecosystems are characterized by the pulse-reserve paradigm, in which a biologically significant precipitation event triggers a pulse of growth that leads to reserves, such as clonal growth or seed production (Noy-Meir 1973; Reynolds et al. 2004; Collins et al. 2008b). Over the growing season, plants integrate multiple pulse events, a phenomenon referred to as higher-order pulses (Schwinning and Sala 2004), leading to hierarchical pulse dynamics whereby precipitation events scale over time to drive state transitions in aridland ecosystems (Collins et al. 2014). From the standpoint of community dynamics, hierarchical pulse dynamics describes how abiotic factors drive within- and between-year temporal variability, whereas the HRF predicts that communities will change over time via acclimation, community reordering, and species turnover. Together, these models emphasize the significant role played by bottom-up resources and shifting species abundances in driving temporal variation and community dynamics in the absence of disturbance.

Under current and likely future conditions, the interplay of local hotspots of change and boundary dynamics will generate large-scale vegetation mosaics that are constantly changing (and pulsing) at different rates in response to chronic changes in environmental drivers in the absence of disturbance. Therefore, aggregate properties of plant communities (cover, biomass, stem density) may reach a dynamic steady state (Bormann and Likens 1979), but

compositional change (species reordering) within a community type may mask instabilities within an alternative-stable-state framework (Scheffer et al. 2012; D'Odorico et al. 2013). That is, vegetation may remain in an apparently stable state despite a strong reordering of abundances of dominant species, yet such a shift in abundances may ultimately destabilize the system and facilitate a state change. Moreover, relatively rapid vegetation change in the absence of disturbance may increasingly occur as a consequence of dynamic hotspots and shifting patch boundaries over space and time in response to chronic alterations in abiotic drivers, many of which are the product of global environmental change.

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View of a desert grassland ecotone, looking toward the northeast at the Sevilleta National Wildlife Refuge, New Mexico. In the foreground, creosote bush is encroaching into grassland dominated by the Chihuahuan Desert grass black grama. The lighter-colored grassland in the distance is dominated by the shortgrass steppe species blue grama. Creosote bush does not invade areas dominated by blue grama. The abundance of black grama has more than doubled across this ecotone during the past 25 years. Photo by Scott Collins.