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SPECIAL FEATURE ARTICLE

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Press–pulse interactions and long-term community dynamics in a Chihuahuan Desert grassland

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Abstract

Questions: Reordering of dominant species is an important mechanism of community response to global environmental change. We asked how wildfire (a *pulse* event) interacts with directional changes in climate (environmental *presses*) to affect plant community dynamics in a Chihuahuan Desert grassland.

Location: Sevilleta National Wildlife Refuge, Socorro County, New Mexico, USA.

Methods: Vegetation cover by species was measured twice each year from 1989 to 2019 along two permanently located 400-m long line intercept transects, one in Chihuahuan Desert grassland, and the second in the ecotone between Chihuahuan Desert and Great Plains grasslands. Trends in community structure were plotted over time, and climate sensitivity functions were used to predict how changes in the Pacific Decadal Oscillation (PDO) affected vegetation dynamics.

Results: Community composition was undergoing gradual change in the absence of disturbance in the ecotone and desert grassland. These changes were related to the reordering of abundances between two foundation grasses, *Bouteloua eriopoda* and *B. gracilis*, that together account for >80% of above-ground primary production. However, reordering varied over time in response to wildfire (a *pulse*) and changes in the PDO (a *press*). Community dynamics were initially related to the warm and cool phases of the PDO, but in the ecotone these relationships changed following wildfire, which reset the system.

Conclusion: Species reordering is an important component of community dynamics in response to ecological presses. However, reordering is a complex, non-linear process in response to ecological presses that may change over time and interact with pulse disturbances.

KEYWORDS
Bouteloua eriopoda, *Bouteloua gracilis*, climate change, desert grassland, fire, Pacific Decadal Oscillation, species reordering

1 | INTRODUCTION

Most ecological communities are undergoing directional change in response to a variety of natural and anthropogenic forces even in the absence of disturbance (Blowes *et al*., 2019). These forces include environmental *presses*, such as climate change or N deposition, that occur over the long term. Presses can elicit gradual change in ecological communities toward tipping points at which the system abruptly switches from one ecosystem state to another (Beisner *et al*., 2003). In contrast, disturbance (*pulse*) events, defined as relatively discrete events (e.g., wildfire) that reduce dominance and free up resources (Jentsch and White, 2019), can cause abrupt changes in composition that may initiate recovery processes or also result in a new alternative stable state (e.g., Scheffer *et al*., 2001; Allen *et al*., 2015). Given the pervasiveness of both forces, it is likely that presses and pulses will frequently interact to affect the dynamics and stability of ecological communities now and in the future (Scheffer *et al*., 2001).

Under the Hierarchical Response Framework (Smith *et al*., 2009) ecosystems respond to environmental presses through a series of processes, starting with phenotypic plasticity of individuals, followed by a reordering of dominance (rank abundance) among species, and finally by species turnover via colonization and local extinction. Phenotypic responses can be relatively rapid but are unlikely to generate persistent change in ecosystem processes over time. Species turnover, via dispersal and establishment, could take decades to occur, especially in ecosystems dominated by long-lived species. Thus, community reordering, a change in the ranking of extant species abundances (Avolio *et al*., 2019), may be a key mechanism for community change at intermediate (multi-year) time scales.

Reordering among dominant species within and among functional groups may be a critical process for understanding how ecological communities will respond to global environmental change (Magurran *et al*., 2010; Gravel *et al*., 2016). Reordering may occur among species in similar or different functional groups (grasses, forbs, legumes) under ecological presses and pulses. Moreover, species within the same functional group can differ widely in their biotic interactions, traits, and influence on ecosystem processes (e.g., Magurran and Henderson, 2010; Griffin-Nolan *et al*., 2019). For example, reordering of species led to changes in total above-ground net primary production (ANPP) in a long-term irrigation experiment (Collins *et al*., 2012; Knapp *et al*., 2012), and reordering was shown as the primary driver of community composition change across taxa in a long-term observational study (Jones *et al*., 2017).

Predicting how plant communities respond to global environmental change requires understanding differential sensitivities of species not only to mean trends in global environmental drivers, but also to change in the variability around the mean (Rudgers *et al*., 2018; Gherardi and Sala, 2019). Dry grasslands in the southwestern US can be especially sensitive to climate variability (Knapp and Smith, 2001; Gherardi and Sala, 2019) as well as to disturbances, such as exceptional drought or fire (Parmenter, 2008; Knapp *et al*., 2015). Because these systems are primarily water-limited, precipitation can strongly regulate ecosystem processes in drylands (Collins *et al*., 2008b, 2014; Knapp *et al*., 2015). Major climate drivers in the southwestern US include the annual North American Monsoon, which regulates summer precipitation, and the El Niño Southern Oscillation (ENSO), which varies over three- to six-year intervals and influences winter/spring precipitation. In addition, the Pacific Decadal Oscillation (PDO), a 10- to 20-year ENSO-like pattern of Pacific sea surface variability (Zhang *et al*., 1997), modulates the ENSO generating decades-long cycles between dry and wet conditions (Gutzler *et al*., 2002; Petrie *et al*., 2014). In the southwestern US, precipitation typically increases during the warm phase of the PDO. Around 1998, the PDO started to transition to the cool phase, corresponding to a period of prolonged regional drought and years of low productivity, especially during the early 2000s (Breshears *et al*., 2005; Muldavin *et al*., 2008). From 2013 to 2015, the PDO transitioned back to the warm phase (Meehl *et al*., 2016) portending a likely increase in annual precipitation over approximately the next two decades, consistent with regional rainfall trends over the past ~450 years in response to the PDO (Milne *et al*., 2003).

In addition to climate fluctuations driven by ENSO and the PDO, the southwestern US has experienced an increase in mean annual temperature (Gutzler and Robbins, 2011), but no change in mean annual precipitation during the summer monsoon over the past 100 years (Petrie *et al*., 2014). As a consequence of the increase in mean annual temperature, aridity has increased over the last century (Gutzler and Robbins, 2011). Furthermore, Rudgers *et al*. (2018) found that both mean and variability in aridity increased in central New Mexico, USA, over the past 100 years. Changes in mean and variance of aridity were strongly related to differential, non-linear responses of net primary production in Great Plains grassland dominated by blue grama (*Bouteloua gracilis*) versus Chihuahuan Desert grassland dominated by black grama (*B. eriopoda*). Under wetter/cooler conditions, increasing climate variability favored production in Great Plains (blue grama) grassland, whereas under hotter/dryer conditions greater variability favored Chihuahuan Desert (black grama) grassland. Thus, the current trend of increasing aridity and variability is likely to accelerate reordering of these dominant grasses where they co-occur.

In this study, we used long-term species composition data from two 400-m-long line intercept transects, one in desert grassland dominated by black grama and the other in an ecotone where both blue and black grama co-occur, in central New Mexico, USA, to quantify how increasing aridity (an ecological *press*) and wildfire (an ecological *pulse*) interact to affect species reordering and community dynamics. Prior to a wildfire in 2009, abundance of black grama in the ecotone grassland was increasing at more than twice the rate of blue grama over a 20-year period (Collins and Xia, 2015). However, unlike blue, black grama is highly sensitive to fire. Therefore, natural disturbances, such as wildfire, might reverse the trajectory of change across this ecotone, despite background increases in aridity. We focused on responses by the two dominant grasses because these foundation species govern community structure and ecosystem functioning in this system (Peters and Yao, 2012). Here, we addressed the following questions: (a) is community composition undergoing directional change in the absence of disturbance, and how does fire affect these dynamics; (b) is reordering of dominant species a consistent driver of directional change, and are these changes related to cycles of the PDO; (c) do species-specific sensitivities to the average and variability in climate aid in predicting the reordering process?

2 | METHODS

2.1 | Study site

This study was conducted from 1989 through 2019 at the Sevilleta National Wildlife Refuge (SNWR, latitude 34°20′ N and longitude 106°43′ W), Socorro County, New Mexico, USA. As noted above, two grassland communities occur in the SNWR separated by a narrow ecotone — Chihuahuan Desert grassland to the south and Great Plains grassland to the north (Hochstrasser *et al*., 2002). Together, the two grasses that dominate, blue and black grama, account for>80% of total plant cover (Collins and Xia, 2015), and they influence the abundances of subdominant species (Peters and Yao, 2012; Mulhouse *et al*., 2017). Other common species at this site include scattered shrubs or subshrubs (e.g., *Yucca elata* and *Ephedra torreyana*), as well as a mix of other grasses (e.g., *Pleuraphis jamesii*, *Sporobolus* spp., *Aristida* spp.) and some common forbs (*Machaeranthera* spp., *Astragalus* spp., *Sphaeralcea* spp. *Chaetopappa ericoides*, *Solanum elaeagnifolium*, *Hoffmannseggia drepanocarpa* and *Melampodium leucanthum*) (Mulhouse *et al*., 2017). Soils are Typic Haplargids derived from piedmont alluvium. Soil texture in the upper 20 cm, where highest root biomass occurs (Kurc and Small, 2007), is 68% sand, 22% silt, and 10% clay, with 2% calcium carbonate (Kieft *et al*., 1998). Water-holding capacity and nutrient reserves are very low (Zak *et al*., 1994), and these soils are highly erodible when vegetation cover is removed following fire (Ravi *et al*., 2007).

Although congeners, the two dominant grasses differ in a number of key functional traits. Black grama is a shallow-rooted, perennial, C_4 grass that spreads primarily via stolons (Fields *et al*., 1999). Blue grama, on the other hand, is a long-lived, perennial, C_4 bunchgrass (Gibbens and Lenz, 2001) that grows via basal tillering and often forms rings (Ravi *et al*., 2008). Populations of both species also exhibit considerable local genetic variability indicative of sexual reproduction (Whitney *et al*., 2019; Hoffman *et al*., 2020).

The climate of the region is mid-elevation continental, with relatively hot summers and cold winters. Average annual temperature is 13.2°C (average daily temperature is 1.6°C in January and 25.1°C in July). Average annual precipitation at the site is ~250 mm, ~60% of which occurs during the summer monsoon that typically extends from early July through early September (Notaro *et al*., 2010). Remaining precipitation comes as a mixture of snow and rain during fall, winter and early spring.

2.2 | Vegetation sampling

We measured vegetation cover by species in May and September each year from 1989 to 2019, along two permanently located 400-m long line intercept transects (Collins, 2020). Each transect, one in Chihuahuan Desert grassland (hereafter referred to as desert grassland) dominated by black grama, and one in the ecotone between Chihuahuan Desert and Great Plains grassland (hereafter referred to as ecotone) where black and blue grama co-occur, was oriented north–south, with the end of the ecotone transect located approximately 0.5 km north of the start of the desert grassland transect. In August 2009, a lightning-caused wildfire burned all of the ecotone transect where strong reordering had been occurring, but not the more stable desert grassland transect. To sample vegetation cover in each site, a 100-m measuring tape was affixed to the 0-m rebar stake 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 spaced 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) encountered along the line was recorded at 1 cm resolution, noting the place the species or substrate first crossed the tape. Plants 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 or substrate. Thus, there are no gaps in the data stream along each transect. This procedure was then repeated for each of the remaining three 100-m long segments along each 400-m sampling transect. These transects have been sampled annually in spring and fall since 1989 yielding a very high-resolution data set on species composition and vegetation change under increasing aridity and climate variability over the past 30 years. We used start–stop distances by species to determine total cover for each species along each transect in each year. The maximum cover value (May or September) recorded for each species along each transect was used to assess community structure and dynamics.

2.3 | Data analysis

In the following sections, analyses were organized in relation to phases of the PDO and fire. Ecotone analyses were partitioned as follows: from 1989 to 1998 during the prior warm phase of the PDO, from 1999 to 2008 during the cool phase of the PDO and prior to the wildfire, and during post-fire recovery from 2009 to 2019, which occurred over the most recent transition from the cool to warm phase of the PDO. At the desert grassland site, which did not burn, the analyses were partitioned from 1989 to 1998 (warm phase of PDO), 1999 to 2014 (cool phase of the PDO), and 2015 to 2019 (warm phase of the PDO).

2.4 | Is community composition undergoing directional change in the absence of disturbance, and how does fire affect these dynamics?

To address this question, we used separate two-axis non-metric multidimensional scaling (NMDS) ordinations to visualize long-term community dynamics for the desert grassland and ecotone transects. In addition, species richness and total cover of grasses and forbs were calculated at the transect scale and plotted by year to visualize how fire and climate affected these components of the vegetation. We then used perMANOVA with unrestricted permutation of raw data to determine whether community composition differed pre- and post-fire in the ecotone grassland, or between the warm and cool phases of the PDO in the ecotone and desert grasslands.

2.5 | Is reordering a consistent driver of directional change and if so, are these dynamics related to the PDO cycle?

To answer this question, we correlated changes in the abundance of the dominant grasses with year, and with year partitioned by the different phases of the PDO. Abundance of the dominant perennial grasses can change via two quantifiable mechanisms, a change in the number of "individuals" (by clonal reproduction, seed reproduction, or death) and by a change in the average size of individuals. In this case, an individual is a segment of the line intercept tape covering a species. Obviously, the tape intersects both the edge and center of individual grass clones, 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 blue and black grama across each 400-m transect. We used linear regression to determine whether the abundance of the dominant species, average size of dominants, or number of individual clones changed over time, and how those changes were affected by fire at the ecotone site. We then used ANOVA to determine whether these variables differed pre- and post-fire (ecotone grassland transect) or during the warm and cool phases of the PDO (desert grassland transect).

2.6 | Do species-specific sensitivities to the average and variability in the PDO aid in predicting the reordering process?

Finally, to answer this question, we used a long-term *biomass* data set and climate variables collected at multiple sites across this grassland from 1999 to 2019 to explore how above-ground biomass of black and blue grama correlated with changes in the PDO Index. We related peak fall biomass of blue and black grama to the average PDO Index during each growing season (March–September) each calendar year from 1989 to 2019.

For this analysis, we used data from replicated 1-m^2 permanent plots, rather than line transect data, because these widely distributed quadrats covered a much broader range of climate and environmental conditions than the line intercept transects, maximizing our ability to make inferences about the relationship of the dominant grasses to the PDO. Peak biomass was estimated for each species using a non-destructive volumetric method that estimates biomass allometrically via linear regression models developed for each species over multiple years from plants collected outside of the permanent sampling plots (Muldavin *et al.*, 2008; Rudgers *et al.*, 2019). In each permanently located 1-m^2 plot, we measured percentage cover and height (to the nearest cm) for all individual plants at peak biomass (September) in each year, then used these data to predict live biomass for each species in each quadrat. For black grama, this included 2,404 plot by year combinations; blue grama had 1,280 plot by year observations. Only quadrats in which the grasses occurred were used in these analyses.

We determined PDO climate sensitivity functions (Rudgers *et al.*, 2018) using linear and non-linear regressions of peak biomass against the six-month averaged PDO Index. Because plants were repeatedly measured in permanent plots, we included the random effects of both sampling site, quadrat and year to account for non-independence of observations. Mixed effects models were fit via maximum likelihood using lme in package<nlme> (Pinheiro *et al.*, 2018, R Core Team, 2018). We selected the best model from among a linear, quadratic, or cubic model via model selection procedures with the *AICc* criterion and determined marginal and conditional r^2 values (Burnham and Anderson, 2002).

3 | RESULTS

3.1 | Community dynamics

3.1.1 | Ecotone grassland

From 1989 through 2008 this grassland community was undergoing weak directional change, with some degree of year-to-year fluctuations in community composition (Figure 1a). Community change also occurred during the cool phase of the PDO from 1999 through 2008. The wildfire in 2009 altered community composition, which exhibited post-fire dynamics during the cool and warm phases of the PDO from 2009 through 2015 and from 2015 through 2019, respectively. This community has been relatively stable over the past five years despite a likely transition to the warm phase of the PDO around 2015. Based on perMANOVA results, overall community composition at the ecotone differed significantly pre- versus post-fire (pseudo-F = 4.93, p = 0.0021), and in the warm and cool phases of the PDO (pseudo-F = 11.73, p = 0.001).

3.1.2 | Desert grassland

Grassland composition at this site also showed weak directional change from 1989 through 1999 during the last warm phase of the PDO (Figure 1b). Community change shifted to an alternate state when the PDO changed to the cool phase from 1999 through 2015. Although this transect was not burned in 2009, community composition nevertheless has again undergone directional change primarily during the cool phase of the PDO. After the PDO switched back to the warm phase in 2015, community composition has continued on a trajectory away from the prior state during the previous warm phase

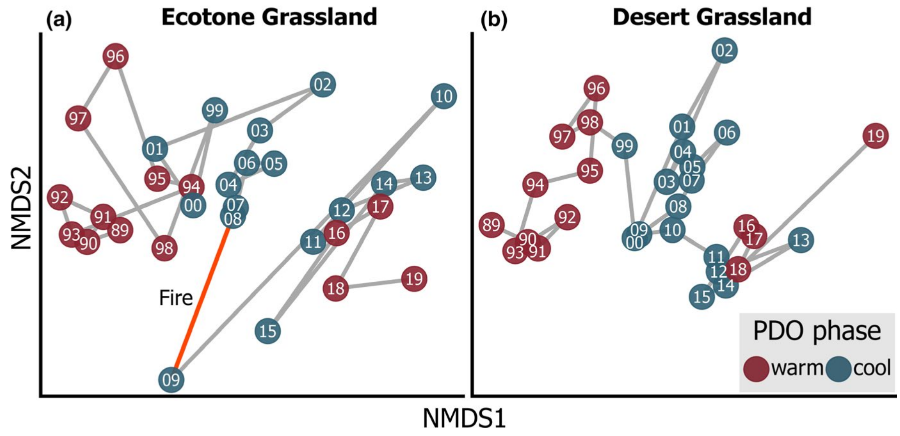

FIGURE 1 Non-metric multidimensional scaling (NMDS) ordinations of community composition from two 400-m long line intercept transects (Desert Grassland and Ecotone Grassland) in the Sevilleta National Wildlife Refuge, New Mexico, USA. Colors correspond to the warm and cool phases of the Pacific Decadal Oscillation. Numbers correspond to years starting in 1989 and ending in 2019. A wildfire burned through the ecotone transect in August 2009 (red line). Stress values were 0.18 and 0.19 for the Ecotone and Desert grasslands, respectively

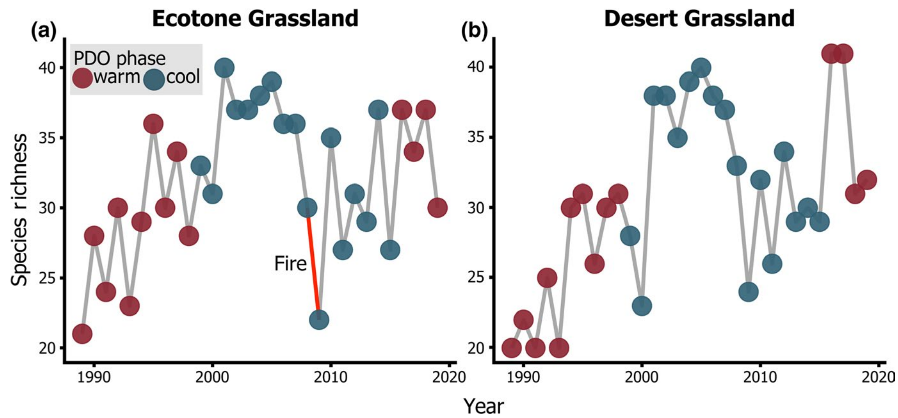

FIGURE 2 Plant species richness from 1989 through 2019 along two 400-m long line intercept transects, one in desert grassland dominated by *Bouteloua eriopoda* and one in an ecotone area where *B. eriopoda* and *B. gracilis* co-occur in the Sevilleta National Wildlife Refuge, New Mexico, USA. Colors correspond to the warm and cool phases of the Pacific Decadal Oscillation. A wildfire burned through the ecotone transect in August 2009 (red line)

of the PDO from 1989 through 1998. Based on perMANOVA results, overall community composition differed significantly between the warm and cool phases of the PDO (pseudo-F = 11.73, p = 0.001).

3.2 | Species richness

Species richness was relatively low along both transects during the first five years of data collection (Figure 2). From 1994 through 2019 mean annual species richness along each 400-m transect was 32.5 + 5.2 *SD* at the ecotone and 33.1 + 4.5 *SD* in the desert grassland. Annual species richness over time was highly correlated between the two sites (r = 0.66, p < 0.001) yet species richness was not correlated to monsoon or annual precipitation at either site (p > 0.06 in both cases). At both sites, species richness declined dramatically in 2009, the year of the wildfire. However, mean species richness across years did not differ pre- (32.0 ± 5.5 *SD*) versus post-fire (32.4 ± 4.1 *SD*) at the ecotone ($F_{1,29}$ = 0.04, P = 0.84), nor in the desert grassland between the warm (28.6 ± 6.9 *SD*) and cool (32.5 ± 5.4 *SD*) phases of the PDO ($F_{1,29}$ = 3.17, p = 0.09).

3.3 | Functional types

Total vegetation cover along each 400-m line intercept transect averaged 192.7 meters (± 60.3 *SD*) and 221.4 meters (± 43.4 *SD*) at the ecotone and desert grassland, respectively, from 1989 through 2019. Grasses accounted for 84.6 ± 4.8% and 87.0 ± 11.2% of total cover at the ecotone and desert grasslands, respectively. Total cover of grasses generally increased at the ecotone until the wildfire in 2009. Grass cover at the ecotone declined 96% between 2008 and 2009, directly after the fire, and 41% between 2008 and 2010, after one year of recovery (Figure 3a). Grass cover then peaked in 2013, a year with high monsoon rainfall. Grass cover did not decline along the unburned desert grassland transect in 2009 but cover also peaked in 2013 (Figure 3b). Grass cover then declined and remained relatively constant from 2014 through 2019 at both sites. Grass cover was positively correlated to monsoon precipitation in the ecotone (r = 0.23, p = 0.009) but not in the desert grassland (r = 0.07, p = 0.172).

Forbs accounted for 6.3 ± 5.2% *SD* and 9.7 ± 11.7% *SD* of total cover at the ecotone and desert grassland, respectively. Forb cover

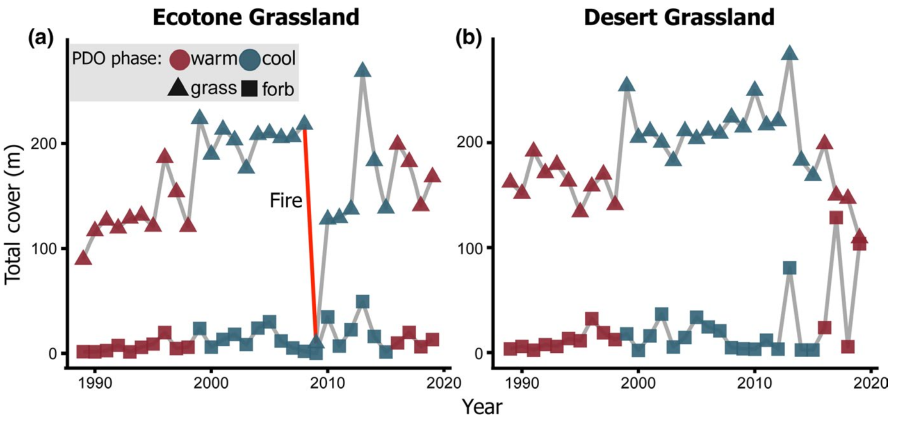

FIGURE 3 Cover of grasses and forbs from 1989 through 2019 along two 400-m long line intercept transects, one in desert grassland dominated by *Bouteloua eriopoda* and one in an ecotone area where *B. eriopoda* and *B. gracilis* co-occur in the Sevilleta National Wildlife Refuge, New Mexico, USA. Colors correspond to the warm and cool phases of the Pacific Decadal Oscillation. A wildfire burned through the ecotone transect in August 2009 (red line)

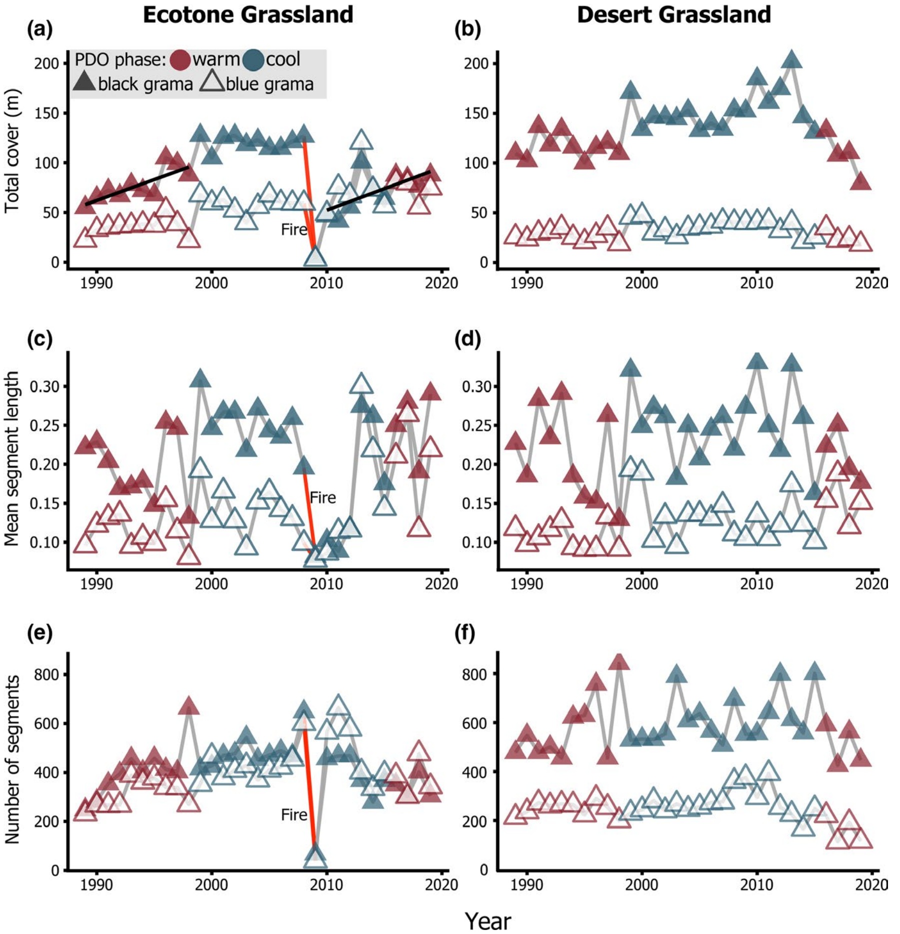

FIGURE 4 Change in abundance, mean number of individuals and mean individual size for black grama (*Bouteloua eriopoda*) and blue grama (*B. gracilis*) from 1989 through 2019 along two 400-m long line intercept transects, one in desert grassland dominated by *Bouteloua eriopoda* and one in an ecotone area where *B. eriopoda* and *B. gracilis* co-occur in the Sevilleta National Wildlife Refuge, New Mexico, USA. Colors correspond to the warm and cool phases of the Pacific Decadal Oscillation. A wildfire burned through the ecotone transect in August 2009 (red lines). Solid line segments in (a) represent significant increases in cover of black grama based on linear regression

was positively correlated with grass cover at the ecotone ($r = 0.27$, $p < 0.005$) but not in the desert grassland ($r = 0.03$, $p > 0.10$). Forb cover was positively correlated to monsoon precipitation at the ecotone ($r^2 = 0.18$, $p = 0.018$) and desert ($r^2 = 0.30$, $p = 0.002$) grasslands.

3.4 | Dynamics of blue and black grama

3.4.1 | Ecotone grassland

Cover of blue grama increased significantly from 40 to 80 m (out of a possible 400 m) across all years from 1989 to 2019 ($r = 0.37$, $p < 0.001$; Figure 4a). Cover of blue grama did not change during the earlier warm phase (1989–1998) of the PDO ($r = 0.07$, $p = 0.45$) nor the cool phase from 1999 to 2008 ($r \sim 0.0$, $p = 0.85$), but did significantly increase from 35.2 to 58.4 m in the PDO cool phase after the fire ($F_{1,18} = 38.1$, $p < 0.001$). Cover of blue grama remained high, 71.2 m, throughout the PDO cool and warm phases following the wildfire from 2010 to 2019, which was a significant increase from its pre-fire cover ($F_{1,29} = 5.67$, $p = 0.02$). Similarly, there was no overall change in cover of black grama from 1989 to 2019 ($r \sim 0$, $p = 0.80$; Figure 4a). During the early warm phase from 1989 to 1998 cover of black grama increased significantly ($r = 0.65$, $p = 0.005$) but, like blue grama, cover of black grama did not change during the cool phase of the PDO from 1999 to 2008 (r ~ 0, p = 0.89), and cover of this foundation species decreased>50% following the wildfire causing a reordering of dominance (Appendix S1). Cover has since fluctuated but generally increased since 2010 (r = 0.45, p = 0.03), whereas cover of blue grama has not increased (r = 0.02, p = 0.70) since the wildfire reversing the reordering process.

Prior to the fire, the average size of blue and black grama individuals was 0.13 and 0.22 m, respectively. After the fire, average size of blue grama individuals increased significantly to 0.18 m ($F_{1,29}$ = 4.29, p = 0.05), whereas average size of black grama individuals remained the same at 0.19 m ($F_{1,29}$ = 1.80, p = 0.19; Figure 4b). Prior to the fire, the average number of individuals of blue and black grama was 369.7 and 446.8 per 400 m, respectively. After the fire, the average number of individuals of blue grama increased significantly to 407.6 per 400 m ($F_{1,29}$ = 0.70, p = 0.41), whereas average number of individuals of black grama decreased significantly to 348.2 per 400 m ($F_{1,29}$ = 6.32, p = 0.02; Figure 4c). The average size of both species has increased steadily, and the average number of individuals has declined since the wildfire in 2009 (Figure 4).

3.4.2 | Desert grassland

Cover of black grama did not change across all years from 1989 to 2019 (r = 0.06, p = 0.182; Figure 4d) with total cover ranging from ~100 m in 1990 to ~200 m in 2013. Total black grama cover was significantly greater ($F_{1,29}$ = 39.0, p < 0.001) during the cool phase of the PDO (152.17 ± 18.6 m) than in the warm phases (113.59 ± 15.1 m). Likewise, cover of blue grama changed little from 1989 to 2019 (r ~ 0, p = 0.8; Figure 4d) but was significantly greater during the cool phase of the PDO ($F_{1,29}$ = 15.4, p < 0.001), increasing from 26.2 ± 5.7 m to 35.6 ± 7.3 m.

During the warm phase of the PDO, the average size of blue and black grama individuals was 0.12 and 0.21 m, respectively (Figure 4e). During the cool phase of the PDO, the average size of blue grama individuals was essentially unchanged (0.13 m; $F_{1,29}$ = 1.23, p = 0.28), whereas average size of black grama individuals increased significantly to 0.25 m ($F_{1,29}$ = 5.50, p = 0.027). Also, during the warm phase of the PDO, the number of individuals of blue and black grama was 237 and 560 per 400 m, respectively (Figure 4f). During the cool phase of the PDO, the average number of individuals of blue grama increased significantly to 276 per 400 m ($F_{1,29}$ = 5.96, p = 0.021), whereas average number of individuals of black grama decreased slightly to 619 per 400 m ($F_{1,29}$ = 2.22, p = 0.14).

3.5 | Climate sensitivity functions

The relationships between above-ground biomass and the PDO Index differed between blue and black grama (species identity * PDO Index, χ^2 = 7.40, p = 0.007; Figure 5; Appendix S2). Black grama had a steeper slope and some evidence in support of a non-linear relationship (quadratic PDO term: p = 0.06; linear model: Beta = 11.8, SE = 5.58, χ^2 = 4.48, p = 0.03). For blue grama, the strength of association with the PDO was weaker, and nearly significantly different from zero (Beta = 5.6, SE = 3.12, χ^2 = 3.27, p = 0.07).

4 | DISCUSSION

Both desert grassland and ecotone communities have been undergoing compositional change in the absence of disturbance, caused primarily by species reordering. However, the rate of change has varied over time and between the ecotone and desert grassland. In the ecotone, dynamics appear to be driven partly by climate presses that shift along with the PDO, in combination with a pulse disturbance, wildfire. We found evidence of reordering among dominant species in the ecotonal community, but the direction of reordering changed with wildfire and climate variability. Following wildfire, both the number of individuals and average plant size of black grama decreased, whereas these parameters increased for blue grama. In contrast, in the desert grassland, which did not burn, black grama increased on three occasions and then gradually declined over time. Species richness initially increased along both transects and then fluctuated over most of the study period. The fire in 2009 negatively affected richness along the ecotone transect but richness recovered rapidly

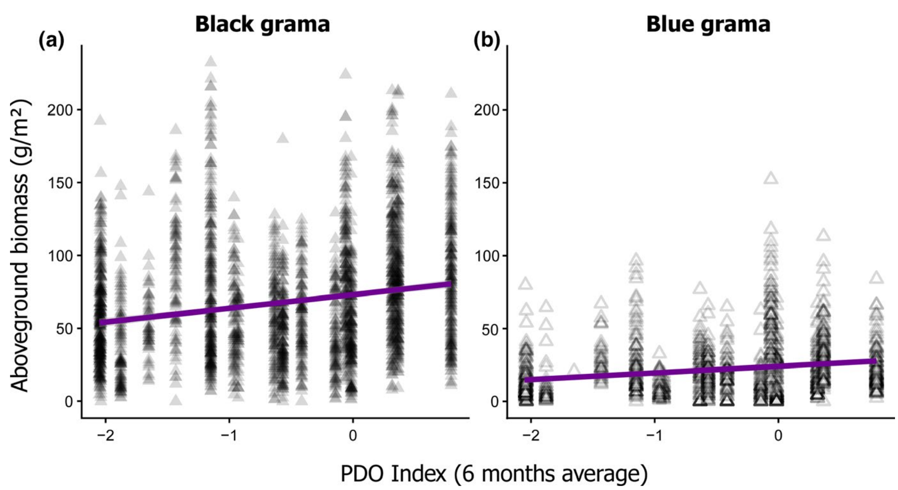

FIGURE 5 Climate sensitivity functions for 13–15 years of above-ground net primary production by (a) blue grama (*Bouteloua gracilis*), and (b) black grama (*B. eriopoda*) in relation to the Pacific Decadal Oscillation (PDO). The Chihuahuan Desert grass, black grama, is more responsive to changes in the PDO than the Great Plains dominant, blue grama. Significance is based on mixed effects models. See *Methods* for details

following the fire. The PDO-based climate sensitivity functions were consistent with the observed temporal patterns of species reordering. These functions suggested that black grama was more sensitive to changes in the PDO than blue grama. If precipitation increases, as expected during the warm phase of the PDO, interannual variability in climate should favor the abundance of black over blue grama. It remains unclear, however, how these dynamics may change as aridity increases under climate change.

Over the 31-year study, cover of black grama increased in some years in both grassland sites (e.g., 1999). Peters and Xao (2012) found that black grama quickly colonized vacant space via stolons following the removal of blue grama in a long-term experiment. Thus, this species is capable of rapid growth when conditions are appropriate. Growth of blue grama, a much longer-lived species (Gibbens and Lenz, 2001), is constrained by its caespitose morphology at this site (Ravi *et al.*, 2008; Hoffman *et al.*, 2020). Following the fire at the ecotone, however, cover of black grama declined to levels less than in 1989 when measurements started, whereas cover of blue grama was unaffected by fire. Prior research has shown that black grama recovers slowly following fire (Parmenter, 2008), whereas abundance of blue grama is generally insensitive to fire (Ladwig *et al.*, 2014). Since the fire, however, black grama has been recovering at a similar rate comparable to its growth from 1989 to 1998, during the prior warm phase of the PDO, whereas cover of blue grama has not changed. It remains to be seen if this pattern will continue under the warm phase when precipitation is generally expected to increase over the next ~2 decades, or if the steep rise in interannual variability in aridity (Rudgers *et al.*, 2018) may increasingly influence these dominant species.

By nearly all outcomes of interspecific interactions, blue grama should be replacing black grama, and yet the opposite has been occurring. In both field and greenhouse experiments, blue grama was a superior competitor to black grama (Peters and Yao, 2012; Chung and Rudgers, 2016). Further, blue grama responded positively to additions of as little as 2 g N m^{-2} $year^{-1}$ reflecting trends in N deposition expected to occur over the next century (Báez *et al.*, 2007), whereas cover of black grama declined after 15 years of high rates of experimental N addition (10 g N m^{-2} $year^{-1}$) at this site (Ladwig *et al.*, 2012). Finally, rates of leaf-level carbon fixation were greater and lasted longer in blue compared to black grama after rainfall pulses in plots where the species co-occurred (Thomey *et al.*, 2014). Only one manipulation has promoted superiority of black grama thus far: black, but not blue, grama increased rapidly under experimental nighttime warming during an above-average monsoon, and average temperatures have warmed in this region over the last century (Gutzler and Robbins, 2011). Thus, black grama is negatively impacted by pulse disturbance (fire) and N fertilization, but can respond favorably to large rainfall pulses and climatic presses (Thomey *et al.*, 2011).

As noted above, reordering is not an orderly process, and the rate of change can be cyclic in response to presses, such as the PDO. Beyond the influence of climate and interspecific competition, an additional hypothesis for reordering dynamics observed here is negative plant–soil feedback (PSF; Bever *et al.*, 1997). Negative PSFs, perhaps operating in conjunction with fluctuations in the PDO, could promote coexistence between these two foundation grasses. Negative feedbacks occur when plants promote the development of microbial communities in their rooting zone and adjacent soil that are more detrimental to themselves than to their competitors (Bever *et al.*, 1997). Negative PSFs increase the strength of intraspecific vis-à-vis interspecific competition, which theory predicts will stabilize species coexistence over the long term (Crawford *et al.*, 2019). Field experiments conducted next to the ecotone transect found evidence for the existence of negative PSFs (Chung *et al.*, 2019). Moreover, the strength of PSF effects was a function of plant frequency, such that the abundance of each foundation species increased when it was rare, which theory predicts will also promote long-term, stable coexistence of competitors (Chesson, 2000). Thus, large-scale, long-term fluctuations in climate (presses) along with local scale, short-term negative PSFs could interact to generate long-term coexistence of these dominant C_4 perennial grasses.

Is there evidence that community reordering matters? As noted earlier, a long-term irrigation experiment in tallgrass prairie led to reordering among dominant grasses (Collins *et al.*, 2012) resulting in a significant increase in net primary production (Knapp *et al.*, 2012). In prairies at Cedar Creek, Minnesota, chronic N addition caused a decline in species richness and a reordering of species abundance rankings over a five- to eight-year period (Tilman, 1987). Under N addition, the non-native, C_3 annual grass, *Agropyron repens*, gained dominance over the native, C_4 perennial grass, *Schizachyrium scoparium* (Collins *et al.*, 2008a). As an ecosystem-scale consequence, total plant production in N plots was less resistant and resilient to a one-year severe drought compared to higher-diversity plots dominated by native grasses (Tilman and Downing, 1994). Furthermore, changes in dominant species under high levels of N addition have reduced net primary production as rapidly growing forbs replace the larger perennial grasses (Isbell *et al.*, 2013).

How might community reordering affect ecosystems in the southwestern US? Over the long term, data suggest that black grama is replacing blue grama as aridity increases; however, fire resets this pattern by dramatically decreasing black grama abundance. For 20 years prior to the fire, black grama increased in the ecotone at a rate twice as fast as blue grama (Collins and Xia, 2015). This change in abundances in response to climate drivers has impacts for carbon dynamics. For example, above- and below-ground production was higher in black compared to blue grama grassland (S.Collins, unpublished). This suggests that reordering (higher cover of black and lower cover of blue grama) would increase above- and below-ground net primary production over the long term, and potentially increase soil carbon content. However, this is not the case. Below-ground standing crop biomass (live plus dead) was 27% higher in blue compared to black grama grassland (J.Holguin *et al.*, unpublished). Less carbon is stored in black grama grassland despite higher above- and below-ground production because ecosystem respiration rates were higher in desert grassland under increasing aridity (Petrie *et al.*, 2015).

In addition to carbon dynamics, woody plant encroachment is an ongoing global phenomenon in which native C_3 shrubs and trees are invading and replacing C_4-dominated grasslands (Eldridge *et al.*, 2011). It has been estimated that nearly 20 million ha of grassland have been invaded by woody species across the southwestern US during the last 150 years (van Auken, 2000). In our system, shrub encroachment occurs primarily in areas dominated by black grama (Peters *et al.*, 2006). If reordering results in black grama replacing blue grama, the stage may be set for further shrub encroachment, which, in turn, may increase carbon sequestration in this region (Petrie *et al.*, 2015). Thus, reordering of the foundation grasses, driven primarily by increasing aridity, has clear consequences for carbon cycle processes along with the potential to facilitate shrub encroachment into grassland.

In conclusion, we found that community composition was undergoing gradual change in the absence of disturbance primarily in response to climate, especially in the ecotone grassland. These changes reflected reordering of abundances between the two foundation grasses that account for>80% of above-ground primary production in this system. Community dynamics were strongly related to the warm and cool phases of the PDO, but these relationships changed following wildfire, a pulse disturbance, which reset the system. None of the patterns reported here would be detectable without high-resolution, long-term data sets. This is especially true for the ecotone transect which was formerly reported to be transitioning from dominance by blue grama to black grama prior to the wildfire in 2009 (Collins and Xia, 2015). Within shorter intervals of this long-term time series, abundance of black grama can be seen as increasing, staying the same or decreasing over time. Moreover, our long-term record of vegetation change allowed us to begin to tease apart how these two dominant species responded to long-term ecological climate presses, the PDO and increasing aridity, and how those presses interacted with a pulse disturbance, wildfire, to not only drive change but also reset the system.

Overall, community reordering is a key process embedded in the Hierarchical Response Framework, but reordering is not an orderly process. Rather, community dynamics reflect the interactions among ecological presses (e.g., climate drivers), pulses (e.g., wildfire) and small-scale species interactions, such as negative PSFs, that can shift reordering processes over the long term. Initial conditions favor one species over the other, and as conditions change, this pattern is reversed. Nevertheless, more attention to the causes and consequences of community reordering is needed because reordering can alter key ecosystem processes and potentially promote transitions to alternative stable states.

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AUTHOR CONTRIBUTIONS

Date were collected as part of the Sevilleta Long-term Ecological Research Program. SLC conceived of the analyses, all authors performed statistical analyses, SLC wrote the first draft and all authors contributed to writing and editing the manuscript.

DATA AVAILABILITY STATEMENT

Raw data are available through the Environmental Data Initiative at https://doi.org/10.6073/pasta/63f506aaf52e7a6ecb3fb296b9e83478

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Proportional change in abundance of the dominant grasses.

Appendix S2. Climate sensitivity function models for *Bouteloua gracilis* and *Bouteloua eriopoda*.

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