

LETTER

Species reordering, not changes in richness, drives long-term dynamics in grassland communities

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Abstract

Determining how ecological communities will respond to global environmental change remains a challenging research problem. Recent meta-analyses concluded that most communities are undergoing compositional change despite no net change in local species richness. We explored how species richness and composition of co-occurring plant, grasshopper, breeding bird and small mammal communities in arid and mesic grasslands changed in response to increasing aridity and fire frequency. In the arid system, grassland and shrubland plant and breeding bird communities were undergoing directional change, whereas grasshopper and small mammal communities were stable. In the mesic system, all communities were undergoing directional change regardless of fire frequency. Despite directional change in composition in some communities, species richness of all communities did not change because compositional change resulted more from reordering of species abundances than turnover in species composition. Thus, species reordering, not changes in richness, explains long-term dynamics in these grass and shrub dominated communities.

Keywords

Community dynamics, desert grassland, desert shrubland, fire, species reordering, species richness, tallgrass prairie.

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INTRODUCTION

Variability and change are fundamental characteristics of ecological communities, given sufficient time. Today, ecologists increasingly focus on the causes of variability (e.g. climate change) as well as how communities respond to variability over time. In general, communities may exhibit stochastic change around a loose equilibrium as a function of environmental variability (Bagchi *et al.* 2013; Matthews *et al.* 2013; Renner *et al.* 2014), such as interannual precipitation, or change directionally following disturbance or in response to ecological presses, such as increasing aridity or nitrogen deposition (Sala *et al.* 2000; Avolio *et al.* 2014; Hoover *et al.* 2014). Furthermore, community change may gradually track subtle changes in the environment, or shift abruptly as environmental drivers approach ecological thresholds potentially crossing a tipping point (Scheffer *et al.* 2001; Bestelmeyer *et al.* 2011).

Many aspects of communities may change in response to environmental drivers and a number of indices have been used to quantify these changes. Alpha diversity (species richness) is a widely used measure of community structure (Leibold *et al.* 2017). Yet, richness alone may obscure other dynamics, such as turnover defined as the rate at which species appear and disappear over time (Cleland *et al.* 2013). A less well-documented but potentially important indicator of community response to chronic environmental drivers is species reordering, or the changes in the relative abundances of species within a community over time. Reordering can occur even in the absence of species turnover (Collins *et al.* 2008; Smith *et al.* 2009). All these indices are potentially useful and complementary measures of how ecological communities respond to disturbances or changes in environmental drivers.

Although disturbances are well-known causes of ecological dynamics, many communities are changing in response to environmental drivers in the absence of disturbance, such as nitrogen deposition or elevated levels of atmospheric CO₂ concentration. The Hierarchical Response Framework (Smith *et al.* 2009) proposes that communities will exhibit either linear or nonlinear responses to chronic changes in environmental drivers through multiple processes, including phenotypic plasticity of individuals at relatively short time scales, as well as through a reordering of species dominance patterns along with changes in species composition through colonisation and local extinction (species turnover). Phenotypic change can be relatively rapid, but is unlikely to generate significant change in composition over time. Turnover in species composition via dispersal and establishment could take years to decades to occur, especially in communities dominated by long-lived species. Thus, reordering among dominant species may provide a useful metric for assessing how communities will respond to global environmental change (Magurran *et al.* 2010; Gravel *et al.* 2016).

Change in species composition may or may not be accompanied by changes in species richness. For example increased resource availability may increase dominance and reduce species richness in terrestrial and aquatic communities (Vitousek *et al.* 1997; Elahi *et al.* 2015; Baer *et al.* 2016). In other cases, richness fluctuates around a narrow equilibrium despite changes in composition and abundance (Goheen 2005; Dornelas *et al.* 2014). Such patterns emerge through strong coupling of local communities and regional pools via dispersal, resulting in what has been termed a “carrying capacity” for species richness (Goheen 2005; Ernest *et al.* 2008; Michalet *et al.* 2015). Thus, changes in community composition may be

unrelated to changes in species richness, leading some to suggest that richness is a relatively poor indicator of ecological response to environmental change (Hillebrand *et al.* 2007, 2017).

Two recent meta-analyses have evaluated changes in both species composition and richness over multiple time series (Vellend *et al.* 2013; Dornelas *et al.* 2014). In both cases, most communities exhibited moderate to strong directional change. However, despite these dynamics, there was, on average, no net change in local richness across all the time series. This result was surprising, and has generated considerable debate, given that global biodiversity is declining (Gonzalez *et al.* 2016; Vellend *et al.* 2016). Indeed, it is difficult to draw strong inferences about changes in species richness from time series data that differ among taxa (e.g. phytoplankton, fish, birds), habitats (e.g. tropical forest, open ocean), timeframes (e.g. 1950s vs. 2000s) and lengths of time series (e.g. < 6 to > 50 years).

We analysed long-term, concurrent time series data for plants, grasshoppers, breeding birds and small mammals in arid and mesic grassland-shrubland ecosystems, using long-term abundance- and occurrence-based data sets. Our approach extends those of Vellend *et al.* (2013) and Dornelas *et al.* (2014) by quantifying compositional change driven by turnover and/or changes in species abundances in a variety of taxa measured concurrently that were exposed to common environmental drivers, thereby reducing potential confounding effects arising from different habitats, timeframes and durations. In this case, the drivers are shrub encroachment, which is the consequence of historical grazing and increasing aridity in the arid ecosystem (Van Auken 2000; Rudgers *et al.* unpublished data) and altered fire frequency in the mesic ecosystem (Briggs *et al.* 2005; Ratajczak *et al.* 2014). At both sites, grassland vegetation is undergoing directional change (Collins 2000; Collins & Xia 2015) in plant community composition. Given that vegetation provides structural habitat and food for consumers (Ernest *et al.* 2000; Hovick *et al.* 2014; Duan *et al.* 2016), we hypothesised that the consumer communities would change in concert with vegetation in response to common environmental drivers in each ecosystem.

METHODS

Arid grassland-shrubland

Study site

Our two aridland study sites are located at the Sevilleta National Wildlife Refuge (SNWR), a Long-Term Ecological Research (LTER) site in central New Mexico, USA. The climate is continental, with an average annual temperature of 13.9°C. Precipitation averages ~ 250 mm annually, with ~ 60% falling from July through September in highly localised storms during the summer monsoon, and the rest as winter frontal systems (Gosz *et al.* 1995; Pennington & Collins 2007; Notaro *et al.* 2010).

Sampling methods

The desert grassland site is dominated by the perennial bunchgrasses black grama (*Bouteloua eriopoda*) and blue

grama (*B. gracilis*) (Muldavin 2002; Collins & Xia 2015). The shrubland site is dominated by the long-lived C₃ shrub creosotebush (*Larrea tridentata*), with scattered grasses and forbs found primarily in open spaces between shrubs. Species composition of grassland vegetation was recorded in spring and fall along a 400-m long line-intercept transect established in 1989 and sampled annually through 2008 when the area was burned by a wildfire. Species start-stop distances along the transect were recorded at 1-cm resolution (Collins & Xia 2015). Annual abundance was the highest summed total cover value recorded for each species along the 400-m transect. Grasshopper and small mammal communities were sampled at the grassland and shrubland sites using a web design consisting of twelve 100-m transects radiating from a central point (Parmenter *et al.* 2003). Each site contains five replicate trapping webs (see Table S1 for data summary and sampling dimensions). Small mammal community composition was estimated starting in 1989 using 144 traps placed along each 100-m transect (Wolf *et al.* 2009) on three webs at each site for three nights twice per year. Grasshopper community composition was sampled in spring and fall starting in 1992 by walking along six 100-m long by 1-m-wide strip transects per web ($N = 30$ strip samples) and identifying all grasshoppers encountered to species level. Starting in 1999, shrubland vegetation composition was estimated using four permanent 1-m² plots in the four cardinal directions of each web, for a total of 64 1 m² plots (Muldavin *et al.* 2008). For small mammals and grasshoppers, annual abundance (number of unique individuals) was the average of each species in spring and fall samples. Bird species abundances were taken from Breeding Bird Survey data along the Escondida route located in the SNWR. This transect starts in black grama grassland and ends in creosotebush shrubland. We partitioned abundances on each half of the transect into grassland and shrubland habitat.

Mesic grassland

Study site

Our three mesic study sites are located at the Konza Prairie Biological Station (KPBS), a Long-term Ecological Research site located in the Flint Hills region of northeastern Kansas, USA. The site has a mid-continental climate, with a mean annual temperature of 12.6°C. Mean annual precipitation is ~ 840 mm year⁻¹, 76% of which falls during the growing season from April to September (Knapp *et al.* 2015). KPBS is divided into 64 management units ranging in size from 16 to 133-ha primarily along watershed boundaries. For this study, we used long-term data from three ungrazed management units: annually burned, burned once every 4 years and burned once every 20 years (Table S1). All sites were dominated by native C₄ perennial tall grasses (*Andropogon gerardii*, *Schizachirium scoparium*, *Panicum virgatum* and *Sorghastrum nutans*) and perennial C₃ forbs (*Aster* spp., *Solidago* spp., *Salvia azurea* and *Vernonia baldwinii*). Over the past 15 years, shrub cover (*Cornus drummondii*, *Prunus americana* and *Rhus glabra*) has increased primarily in lowland areas in infrequently burned management units (Briggs *et al.* 2005; Ratajczak *et al.* 2014).

Sampling methods

Vegetation, breeding bird, grasshopper and small mammal communities were all sampled on the same three management units. Vegetation has been sampled in spring and fall of each year since 1984 in five permanently marked 10-m² circular quadrats located along each of four 50-m transects ($n = 20$ quadrats). Cover of each plant species in each quadrat was visually estimated with the Daubenmire cover scale and the abundance of each species at each site was determined by converting the Daubenmire scale to the midpoint of the cover range and averaging across the 20 quadrats (Collins & Calabrese 2012). Breeding passerine birds were sampled by walking along ~1 km permanent transects during June of each year starting in 1981. At 15–20-m intervals along each transect, all individuals seen or heard were counted during a 3–5-min sampling period. Abundance of each species is the total number of individuals counted each year (Powell 2008). Wide-ranging species, such as Red-tailed Hawk (*Buteo jamaicensis*) and other raptors, were not

included in our analyses because their territories may extend beyond the boundaries of our study sites. Grasshopper populations were sampled each year starting in 1984 using 20 sets of 20 sweep samples taken along parallel 10-m transects during the midsummer of each year. Abundance of each species is the total number of individuals collected at each site (Jonas & Joern 2007). Small mammals were sampled from 1982 along permanently located trap lines in each management unit. Each trap line contained 20 stations at 15-m intervals consisting of two large Sherman live traps. Traps were baited with peanut butter and oatmeal on four consecutive nights in spring and fall of each year. Abundance was measured as the average of the spring and fall counts of total number of individuals of each species at each site (Kaufman *et al.* 1998).

Analysis

We used non-metric multidimensional scaling (NMDS) ordinations per taxa to visually assess differences in community

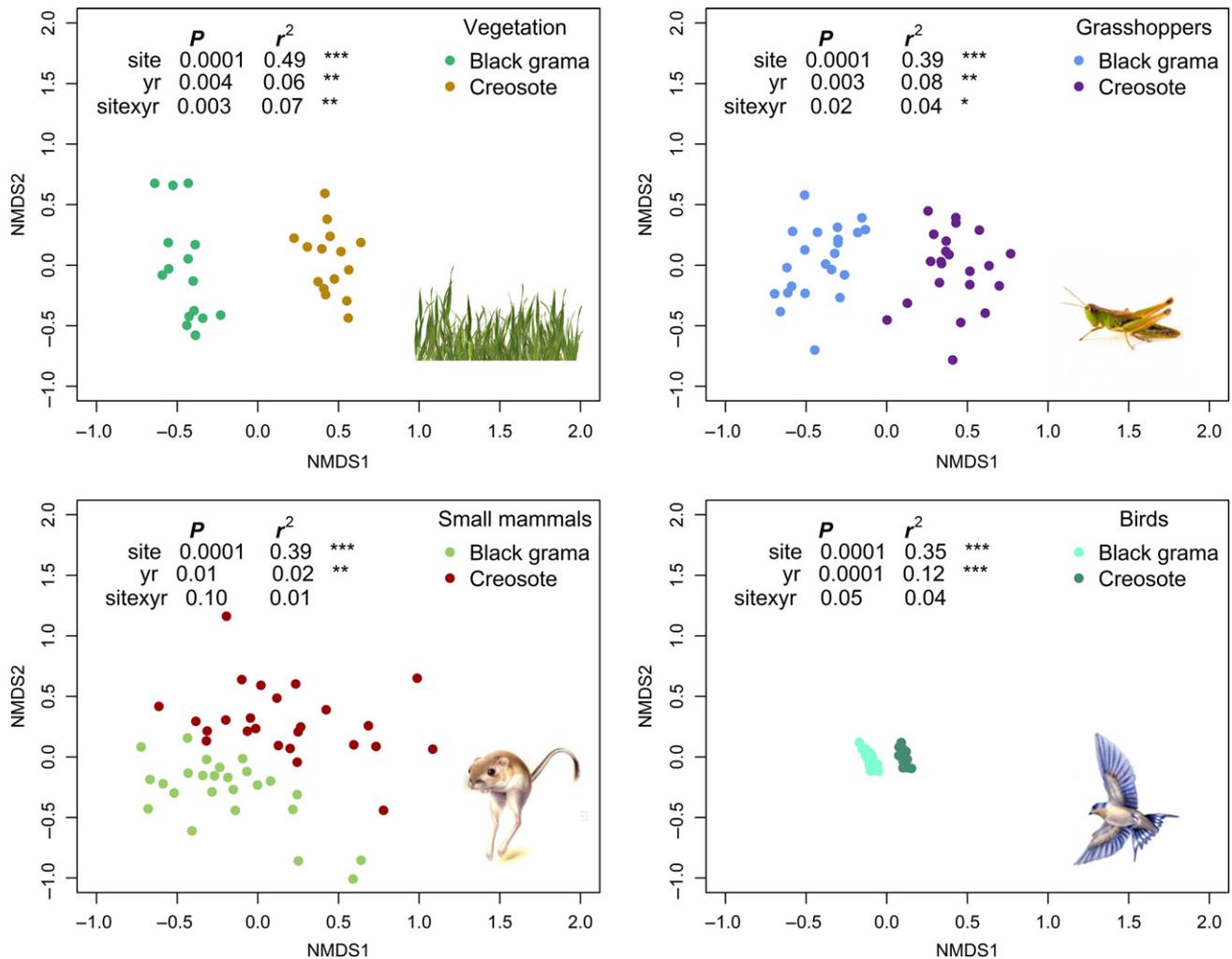


Figure 1 Non-metric multidimensional scaling (NMDS) of vegetation, grasshopper, small mammal and breeding bird community composition between black grama grassland and creosotebush shrubland sites at the Sevilleta National Wildlife Refuge, New Mexico. Each point represents community composition for a given taxon at a site for each sample year (yr). Site is indicated by colour. Inset presents results from PERMANOVA analysis.

composition of each taxonomic group among the two (Sevilleta) or three (Konza) sites in arid and mesic grassland respectively. We then used permutational multivariate analysis of variance (PERMANOVA) using Bray–Curtis dissimilarities to determine if communities of each taxon differed among habitats within a site. Bray–Curtis dissimilarity performs well with relative abundance data in multivariate analyses, such as NMDS and PERMANOVA (Clarke & Warwick 2001, Anderson and ter Braak 2003).

To determine whether communities are undergoing directional change under increasing aridity (Rudgers *et al.*, unpublished data) at Sevilleta and different disturbance regimes (fire frequency) at Konza, and to compare between producer and consumer communities, we calculated the temporal rate of change using time-lag analysis for each taxon in each habitat type at Sevilleta and Konza. Time-lag analysis uses Euclidean distance to measure similarity of community samples at increasing time lags and when regressed, yields an estimate of directional change over time (Collins 2000; Collins *et al.* 2000). The regressions are not used to model relationships, but rather to generate a slope, which reflects rate of change.

Time-lag analysis was calculated and plotted using both abundance and presence-absence data to determine the relative influence of species reordering (abundance data) to species turnover (presence/absence data). If there is positive directional change with abundance data but no change with presence/absence data, then change is driven by reordering among species already present rather than turnover in species composition. We used an analysis of variance (ANOVA) to determine if slopes were significantly different from zero and if slopes within each taxon in each grassland (e.g. grasshoppers between burn frequencies at Konza) were significantly different from each other. In addition, we plotted species richness and turnover through time, and calculated mean rank shifts to further quantify temporal variability. Turnover is a temporal measure of species appearances and disappearances that can affect changes in species richness over time (Diamond 1969). Therefore, we quantified the cumulative number of species appearances and disappearances from one year to the next as a measure of turnover. Mean rank shift (MRS) is a temporal measure of species reordering in a community (Collins *et al.* 2008). MRS is calculated as:

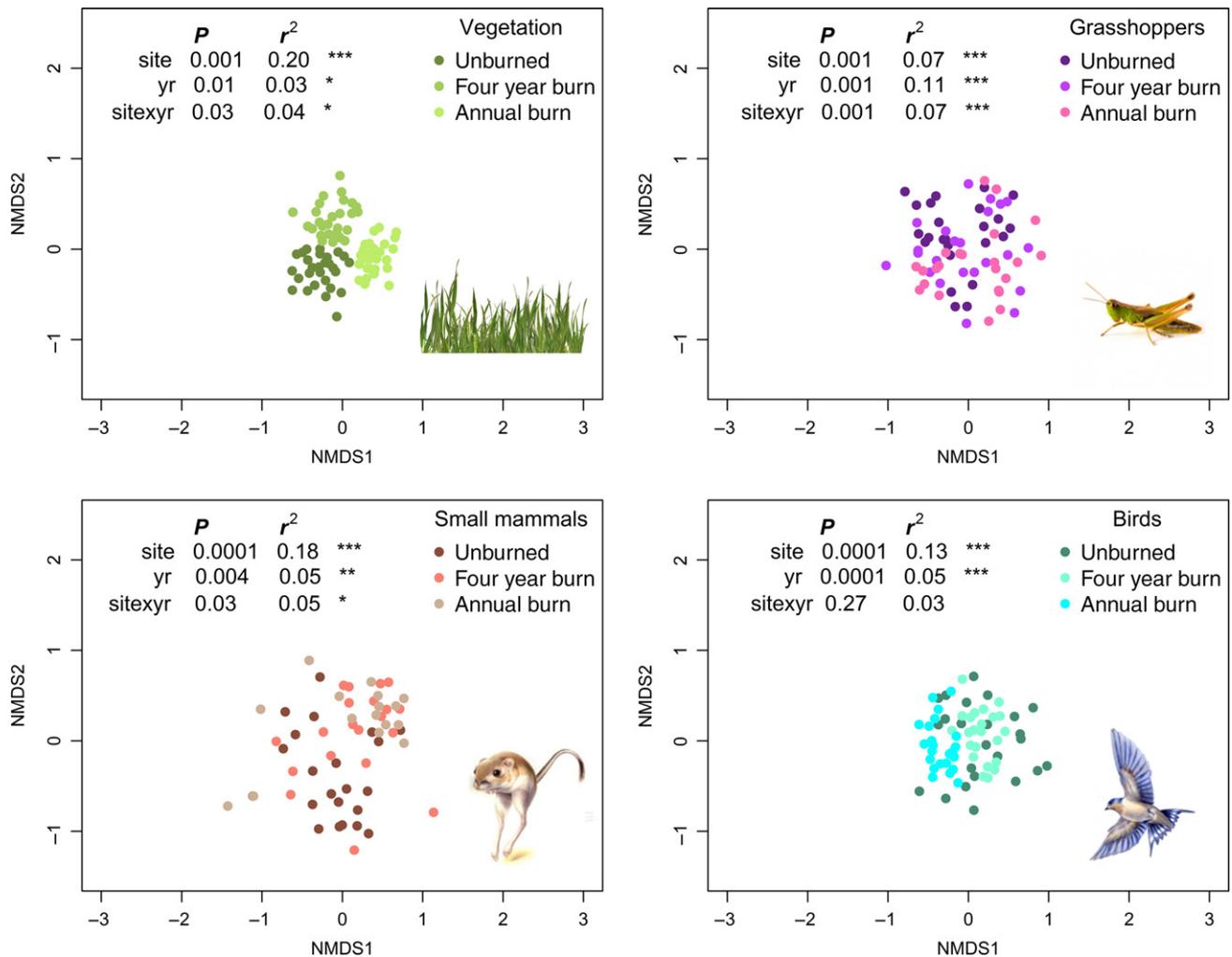


Figure 2 Non-metric multidimensional scaling (NMDS) of vegetation, grasshopper, small mammal and breeding bird community composition of Konza Prairie grasslands that are annually burned, burned once every 4 years or burned once every 20 years. Each point represents community composition for a given taxon at a site for each sample year (yr). Site is indicated by colour. Inset presents results from PERMANOVA analysis.

$$MRS = \frac{n}{i=1} \sum (|R_{i,t+1} - R_{i,t}|) / n$$

where n is the number of species in common in both years, t is year, $R_{i,t}$ is the relative rank of species i in year t . Statistical calculations were performed in R packages *vegan* (Oksanen *et al.* 2016) and *codyn* (Hallett *et al.* 2016).

RESULTS

Sevilleta vegetation and consumer communities showed distinct spatial separation between grassland and shrubland areas for all taxa (Fig. 1) and the PERMANOVA analysis (Fig. 1, inset) showed significant differences in site ($r^2 = 0.35-0.49$ and $P = 0.0001$ for all taxa) and year ($r^2 = 0.02-0.12$ and $P = 0.0001-0.01$) main effects. Only vegetation and grasshopper communities had significant site by year interactions. Konza Prairie vegetation communities also showed spatial separation in the NMDS ordination between fire frequencies. Although consumer communities did not separate visually in ordination space (Fig. 2), PERMANOVA analysis (Fig. 2, inset)

showed significant differences in site ($r^2 = 0.07-0.20$ and $P = 0.0001-0.001$) and year ($r^2 = 0.03-0.11$ and $P = 0.0001-0.01$) main effects for all taxa.

At Sevilleta, most plant and consumer communities exhibited high interannual variability in composition. Despite that variability (Fig. 3, Table 1) strong directional change in relative abundances existed in both black grama grassland (slope = 2.1, $P = 0.014$; Table 2) and creosotebush shrubland (slope = 1.3, $P = 0.002$). Although the rate of change was higher in grassland than shrubland vegetation, differences in rates were not significant ($F = 0.001$, $P = 0.972$; Table 2). As for consumer communities, grassland (slope = 16.3, $P < 0.001$) and shrubland (slope = 21.9, $P < 0.001$) breeding bird communities at Sevilleta were undergoing strong and similar rates of directional change. Grassland (slope = 0.0, $P = 0.887$) and shrubland (slope = -0.0, $P = 0.141$) small mammal communities were relatively stable, especially in creosotebush shrubland where interannual variability was low. Finally, grasshopper communities in grassland are undergoing directional change (slope = 0.9, $P = 0.017$) whereas

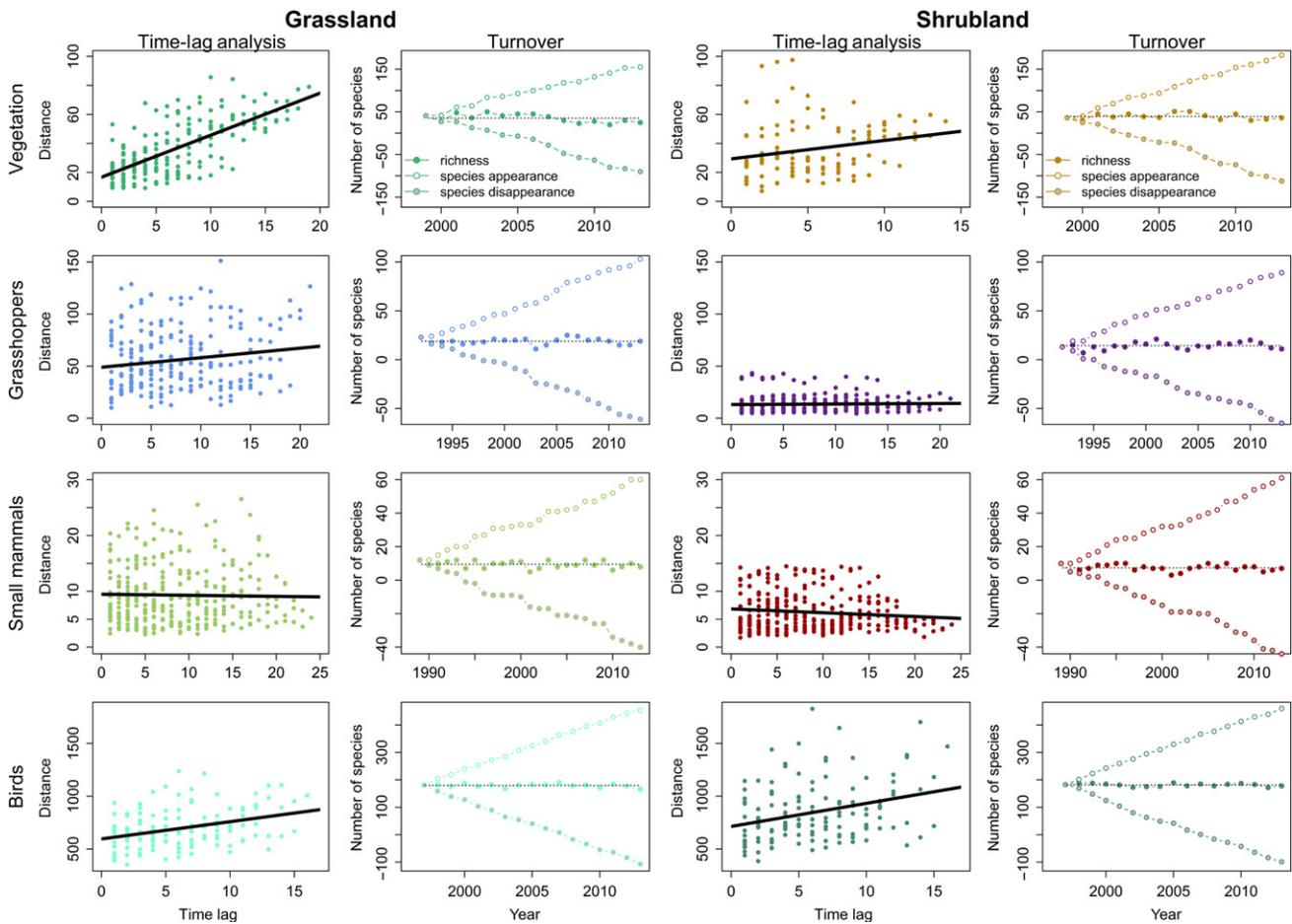


Figure 3 Community temporal dynamics of vegetation, grasshopper, small mammal and breeding bird communities for black grama grassland and creosotebush shrubland at the Sevilleta site. Time-lag analysis depicts the temporal rate of change in community composition by plotting similarity of community samples, using Euclidean distance, at increasing time lags. For regression statistics see Tables 1 and 2. Turnover plots depict total species richness (number of species) and cumulative year-to-year of all species appearances and disappearances. The turnover plots are linear indicating a constant rate of appearances and disappearances over time. In turnover plots, solid symbols are species richness, open symbols are appearances and lightly filled symbols are disappearances.

Table 1 Metrics of temporal dynamics for vegetation, grasshopper, small mammal and breeding bird communities among grassland and shrubland habitats at Sevilleta and fire frequency treatments at Konza Prairie

	Site	Taxa	Time-lag slope	<i>P</i> value	<i>r</i> ²	Species turnover	Mean rank shift
Sevilleta	Grassland	Vegetation	2.1	0.07	0.03	3.0	1.7
Sevilleta	Shrubland	Vegetation	1.3	0.02	0.05	5.0	2.6
Konza	Unburned prairie	Vegetation	0.8	<0.001	0.07	10.4	2.2
Konza	4-yr burned prairie	Vegetation	0.2	0.35	0.002	9.7	2.3
Konza	Annually burned prairie	Vegetation	0.3	0.05	0.01	8.0	2.5
Sevilleta	Grassland	Grasshoppers	0.9	0.02	0.03	3.2	4.0
Sevilleta	Shrubland	Grasshoppers	0.1	0.64	0.0009	3.5	2.2
Konza	Unburned prairie	Grasshoppers	-0.5	0.07	0.01	3.7	1.2
Konza	4-yr burned prairie	Grasshoppers	1.2	0.01	0.009	5.7	0.8
Konza	Annually burned prairie	Grasshoppers	1.4	0.08	0.01	3.7	0.7
Sevilleta	Grassland	Small mammals	0.0	0.72	0.0004	2.0	1.8
Sevilleta	Shrubland	Small mammals	-0.1	0.04	0.01	3.2	1.5
Konza	Unburned prairie	Small mammals	1.2	<0.001	0.3	3.0	0.6
Konza	4-yr burned prairie	Small mammals	0.3	0.06	0.01	3.4	0.5
Konza	Annually burned prairie	Small mammals	0.1	0.14	0.01	2.1	0.5
Sevilleta	Grassland	Breeding birds	16.3	<0.001	0.12	10.7	12.3
Sevilleta	Shrubland	Breeding birds	21.9	<0.001	0.09	7.5	10.8
Konza	Unburned prairie	Breeding birds	0.1	<0.001	0.07	7.5	1.3
Konza	4-yr burned prairie	Breeding birds	0.1	0.001	0.04	5.5	2.2
Konza	Annually burned prairie	Breeding birds	0.1	0.02	0.02	3.8	1.8

Time lag analysis measures rate of community change over time, species turnover is the average proportional change in species from 1 year to the next, and mean rank shift is a measure of how much species reordering of abundances occurs from 1 year to the next. Significance at $P < 0.05$.

grasshoppers in shrubland (slope = 0.1, $P = 0.142$) have high interannual variability and exhibit little directional change.

At Konza, communities also exhibited high interannual variability in composition. Plant (slope = 0.2–0.8; $F = 2.607$, $P = 0.074$), grasshopper (slope = -0.5–1.4; $F = 5.263$, $P = 0.005$) and small mammal (slope = 0.1–1.2; $F = 5.839$, $P = 0.003$) communities were undergoing variable rates of directional change under different fire frequencies (Fig. 4, Table 1). Unburned prairie communities are distinctly different from annually and 4-year burned communities, significantly so in grasshoppers ($P = 0.005$) and small mammals ($P = 0.003$). Breeding birds (slope = 0.1; $F = 0.161$, $P = 0.851$) have weak directional change but with varying amounts of interannual variability (Table 1).

Despite weak to strong directional changes in relative abundances in a number of taxa in both arid and mesic systems, species richness for all taxa at all sites showed minimal change over time. This stability results from comparable levels of appearances and disappearances among taxa over time at each site. Not surprisingly, annual species turnover (Table 1) was highest in communities with higher overall species richness. Mean rank shift (Table 1), a measure of community reordering, was highest for breeding bird communities and lowest for small mammals. To assess the role of reordering vs. turnover we calculated time lag analyses for all sites and taxa using presence–absence data. In all cases slopes were lower than the analyses with abundance data, indicating little to no directional change in species occurrences over time (Figs S1 and S2).

DISCUSSION

We used long-term annual richness and composition data of co-occurring plant, grasshopper, small mammal and breeding bird communities from arid and mesic grasslands to

investigate changes in species richness and composition over time. We found high interannual variability in composition in most communities. Four of the five plant communities (grassland and shrubland at Sevilleta; annual burn and unburned at Konza) exhibited directional change in species composition, yet not all consumer communities were changing in concert with plant communities. Despite directional change in several taxa at each site, species richness of all communities was relatively constant and fluctuated only within a narrow range of variation. This occurred because directional change was primarily driven by shifting abundances of species already in the community, more so than turnover in species composition.

At Sevilleta, grassland vegetation was undergoing strong directional change. This grassland vegetation is experiencing reorganisation as the Chihuahuan Desert grass, *Bouteloua eriopoda*, has doubled in abundance, whereas the co-dominant, *B. gracilis*, has remained relatively stable over time (Collins & Xia 2015). This reordering is a function of higher interannual climate variability under increasing aridity, which favours *B. eriopoda* over *B. gracilis* (Rudgers *et al.* unpublished data). Forbs, on the other hand, tend to fluctuate from year to year in response to seasonal variability in precipitation (Mulhouse *et al.* 2017).

Creosotebush shrubland has been expanding over the past 150 years (Van Auken 2000) by invading areas dominated by *B. eriopoda* (Peters *et al.* 2004). Grass and forb richness and cover decline as the abundance of creosotebush increases (Báez *et al.* 2007), especially following multiyear drought (Báez *et al.* 2013), reflecting the gradual process of species turnover driven by climate variability. In addition, shrub encroachment alters the local microclimate (D'Odorico *et al.* 2010) by creating warmer soil surface temperatures during winter and spring. As a consequence, these two vegetation types support significantly different consumer communities, yet temporal dynamics differ

Table 2 Analysis of variance for time lag slopes between sites for Sevilleta and Konza producer and consumer communities

	Sum Sq	DF	F value	P value
Sevilleta				
Vegetation				
Grassland	2.82	1	6.278	0.014
Shrubland	2.72	1	10.216	0.002
Interaction	0.00	1	0.001	0.972
Grasshoppers				
Grassland	1.70	1	5.831	0.017
Shrubland	0.65	1	2.167	0.142
Interaction	0.12	1	0.418	0.519
Small mammals				
Grassland	0.01	1	0.020	0.887
Shrubland	0.58	1	2.176	0.141
Interaction	0.23	1	0.793	0.374
Breeding birds				
Grassland	1.10	1	19.098	< 0.001
Shrubland	1.27	1	14.556	< 0.001
Interaction	0.00	1	0.043	0.836
Konza				
Vegetation				
Unburned	4.15	1	25.761	< 0.001
4-year burned	0.32	1	1.45	0.229
Annually burned	0.85	1	2.889	0.090
Interaction	1.18	2	2.607	0.074
Grasshoppers				
Unburned	0.67	1	1.102	0.295
4-year burned	9.41	1	10.842	0.001
Annually burned	3.07	1	4.091	0.044
Interaction	7.82	2	5.263	0.005
Small mammals				
Unburned	14.17	1	67.973	< 0.001
4-year burned	1.07	1	2.833	0.094
Annually burned	0.87	1	1.412	0.236
Interaction	4.53	2	5.839	0.003
Breeding birds				
Unburned	0.84	1	15.437	< 0.001
4-year burned	0.91	1	12.066	< 0.001
Annually burned	1.16	1	7.237	0.008
Interaction	0.03	2	0.161	0.851

A significant positive slope indicates directional change over time. A significant size effect indicates that the slope was significantly different from zero. A significant interaction effect indicates that the slopes for a given taxon within a site (e.g. grasshoppers among fire frequencies at Konza) were significantly different from each other. Significance at $P < 0.05$.

among taxa. There is no directional change in small mammal community composition in either vegetation type, whereas breeding birds appear to be undergoing strong directional change in both grassland and shrubland which could be driven to some extent by stochastic processes (Rivers *et al.* 2010; Renner *et al.* 2014) or slow temporal changes occurring over decades (Kampichler *et al.* 2014). Grasshoppers, which include C_3 and C_4 specialists (Engel *et al.* 2009), as well as blue vs. black grama specialists (Rominger *et al.* 2009), are likely tracking changes in food resources in grassland, whereas resource supply in shrubland may be more reliable from year to year resulting in no directional change and low interannual variability. For any cross-taxon congruence occurring within each site, abiotic factors are likely to exert a stronger influence than biotic ones (Duan *et al.* 2016).

Vegetation change occurred across burning treatments at Konza, with the highest rate of compositional change in unburned grassland. Fire is a well-known regulator of vegetation dynamics in tallgrass prairie, with frequent fire reordering rank-abundance of dominant grasses (Collins & Calabrese 2012). Shrub encroachment—itsself a result of decreased fire frequency—gives rise to spatial heterogeneity (Ratajczak *et al.* 2017a,b), triggering changes in community composition of consumers relative to sites with more frequent fire. Indeed, composition and dynamics of grasshopper (Jonas & Joern 2007), breeding bird (Powell 2008) and small mammal communities (Kaufman *et al.* 1998) in ungrazed grassland are mostly affected by fire return interval. In general, as the frequency of disturbance increases, the return tendency to a former state (i.e. resilience) takes longer, if it occurs at all (Matthews *et al.* 2013; Ratajczak *et al.* 2017a).

Our findings extend those of previous studies (Vellend *et al.* 2013; Dornelas *et al.* 2014) reporting directional change in communities despite no net change in local species richness. In many cases, the directional changes they reported could be driven by shifting species abundances alongside constrained variation in species richness. One potential mechanism underlying this pattern is the degree of coupling between local communities and regional species pools (Ricklefs 1987; Gravel *et al.* 2016). Most communities contain only a subset of species from the regional pool, resulting from some combination of dispersal limitation, environmental filters and interactions with extant species that prevent colonisation (Ernest *et al.* 2008). This tight coupling drives non-random compensatory colonisation and extinction dynamics at the local level. As a consequence, species richness may be saturated locally and thus exhibit limited temporal variability (Goheen 2005; Ernest *et al.* 2008; Gravel *et al.* 2016). Therefore, directional change can occur even when species richness remains constant.

In general, our results are consistent with predictions of the Hierarchical Response Framework (Smith *et al.* 2009). We observed strong directional change in aridland vegetation at Sevilleta in the absence of disturbance under increasing aridity. Dynamics of Konza grassland communities were strongly driven by fire return interval, with considerable shrub encroachment occurring under low and intermediate fire frequencies. These changes in plant community composition led to clear differences in consumer communities between grassland and shrubland at Sevilleta, and under different fire frequencies at Konza. Of note, several consumer communities were not undergoing directional change despite relatively strong changes in the vegetation underlying these consumer communities. Others have reported variable responses among taxa to common drivers of ecological change (Duan *et al.* 2016). Thus, temporal change in vegetation is not necessarily predictive of temporal change in co-occurring consumer communities.

Species richness, on the other hand, was remarkably stable for all taxonomic groups in arid and mesic grasslands. Because time-lag analyses of presence-absence data showed little directional change across all taxa, temporal dynamics in these communities primarily reflected reordering of species within the community, with only limited contribution from species turnover. Because directional change primarily results

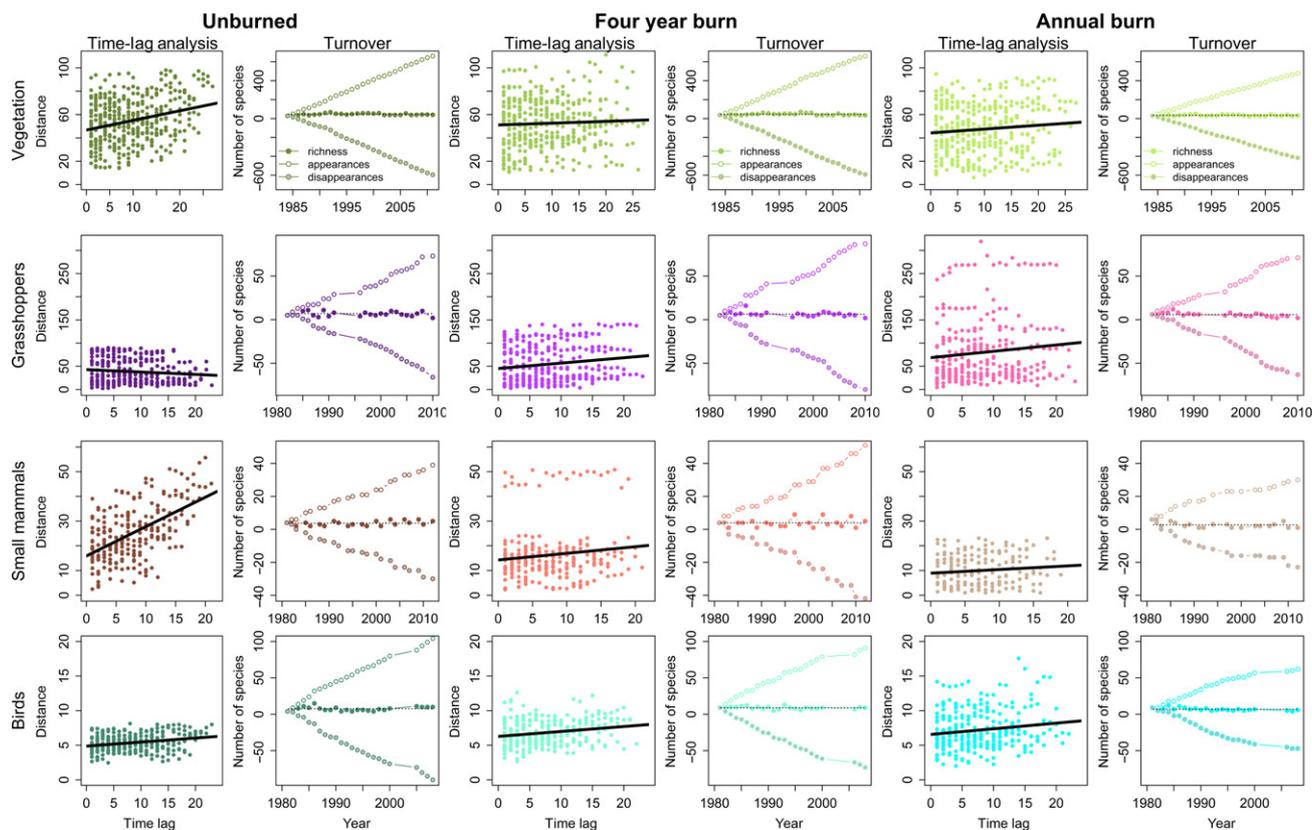


Figure 4 Community temporal dynamics of vegetation, grasshopper, small mammal and breeding bird communities for unburned, 4-year burn and annually burned tallgrass prairie sites at Konza Prairie Biological Station. Time-lag analysis depicts the temporal rate of change in community composition by plotting similarity of community samples, using Euclidean distance, at increasing time lags. For regression statistics see Tables 1 and 2. Turnover plots depict total species richness (number of species) and cumulative year-to-year of all species appearances and disappearances. The turnover plots are linear indicating a constant rate of appearances and disappearances over time. In turnover plots, solid symbols are species richness, open symbols are appearances and lightly filled symbols are disappearances.

from reordering of abundances among species already present, our results reconcile how directional change can occur without concurrent directional changes in species richness (e.g. Vellend *et al.* 2013; Dornelas *et al.* 2014; Pärtel *et al.* 2016). Chronic drivers of global change are likely to affect species abundances and community composition in the future, and our study demonstrates that changes in species abundances and community reordering, rather than changes in species richness, will be a better indicator of the rate and pattern of community response to future global environmental change.

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AUTHORSHIP

SLC and SKJ designed the study. SKJ and JR organised and analysed the data. SKJ and SLC wrote the first draft of the manuscript. All authors contributed substantially to further drafts and revisions.

DATA ACCESSIBILITY STATEMENT

All raw data are currently available via the Sevilleta (<http://sevlternet.edu/>) and Konza Prairie (<http://lter.konza.ksu.edu/>) LTER websites and via the LTER Data Portal (<https://portal.lternet.edu/nis/home.jsp>).

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