

Chapter 8

Using Natural Range of Variation to Set Decision Thresholds: A Case Study for Great Plains Grasslands

Amy J. Symstad and Jayne L. Jonas

Abstract Natural range of variation (NRV) may be used to establish decision thresholds or action assessment points when ecological thresholds are either unknown or do not exist for attributes of interest in a managed ecosystem. The process for estimating NRV involves identifying spatial and temporal scales that adequately capture the heterogeneity of the ecosystem; compiling data for the attributes of interest via study of historic records, analysis and interpretation of proxy records, modeling, space-for-time substitutions, or analysis of long-term monitoring data; and quantifying the NRV from those data. At least 19 National Park Service (NPS) units in North America's Great Plains are monitoring plant species richness and evenness as indicators of vegetation integrity in native grasslands, but little information on natural, temporal variability of these indicators is available. In this case study, we use six long-term vegetation monitoring datasets to quantify the temporal variability of these attributes in reference conditions for a variety of Great Plains grassland types, and then illustrate the implications of using different NRVs based on these quantities for setting management decision thresholds. Temporal variability of richness (as measured by the coefficient of variation, CV) is fairly consistent across the wide variety of conditions occurring in Colorado shortgrass prairie to Minnesota tallgrass sand savanna (CV 0.20–0.45) and generally less than that of production at the same sites. Temporal variability of evenness spans a greater range of CV than richness, and it is greater than that of production in some sites but less in other sites. This natural temporal variability may mask undesirable changes in Great Plains grasslands vegetation. Consequently, we suggest that managers consider using a relatively narrow NRV (interquartile range of all richness or evenness values observed in reference conditions) for designating a surveillance threshold, at which greater attention to the situation would be paid, and a broader NRV for designating management thresholds, at which action would be instigated.

A. J. Symstad (✉)
Northern Prairie Wildlife Research Center, U.S. Geological Survey,
26611 U.S. Highway 385, Hot Springs, SD 57747, USA
e-mail: asymstad@usgs.gov

J. L. Jonas
Department of Forest and Rangeland Stewardship, Colorado State University,
Fort Collins, CO, USA

Keywords Natural range of variation · Great Plains grasslands · Prairie · Plant species richness · Plant species evenness · Diversity · Temporal variability · Surveillance threshold · Management threshold

Introduction

Ecological thresholds are an appealing concept for natural resource management because they provide dramatic, drastic pictures of the consequences of mismanagement to a broad audience. Unfortunately, predicting the conditions that precede the crossing of an ecological threshold is notoriously difficult (Scheffer and Carpenter 2003; Thrush et al. 2009; Hastings and Wysham 2010). Conversely, not all ecosystems exhibit threshold behavior (Stafford Smith 1996; Bagchai et al. 2012), or ecological thresholds may occur far outside the range of conditions maintained by management, as is often the case in protected natural areas like national parks. These conditions do not preclude the establishment of decision thresholds—values of ecosystem state variables that prompt changes in management actions. Instead, managers can establish decision thresholds, also known as action thresholds (Ford et al. 1999), management thresholds (Bennetts et al. 2007), or action-assessment points (Mitchell et al., Chap. 10), based on the natural range of variation (NRV) of the ecosystem attributes they are monitoring.

NRV is a concept with many names, including “range of natural variation,” “historical range of variation,” “natural variability,” and “reference variability,” with some authors preferring “historic” over “natural” because it implies that the effects of indigenous people on ecosystems are included, and because it avoids the ambiguity of the term “natural” (Egan and Howell 2001b). A similar concept is “reference condition,” used frequently in assessing the ecological integrity of streams and wetlands, but with less emphasis on range and variation than the other terms (Stoddard et al. 2006). We use “natural range of variation” to be consistent with Mitchell et al. (Chap. 10). Regardless of its exact name, the concept was developed to recognize that ecosystems are dynamic, but that their dynamics operate within bounds that remain relatively consistent over time (Morgan et al. 1994). To some, it also implies that the ecosystem is self-sustaining within the range of these bounds, but outside the range the system becomes unrecognizable (Egan and Howell 2001b) and, presumably, difficult to return to its original condition. In this context, NRV is related to ecological thresholds, in that it assumes there is a point beyond which an ecosystem will shift to a different state (Groffman et al. 2006). The driver behind this shift can be natural (e.g., a strong hurricane) or anthropogenic (e.g., nutrient enrichment of water bodies from agricultural runoff). Either way, there is no inherent assumption in the concept that the small step from inside to outside a system’s NRV will result in a large, abrupt change in an ecosystem quality, property, or phenomenon (Unnasch et al. 2009).

On the other hand, NRV can also be a useful concept when an ecosystem property is of management interest, but the quality may not change substantially even as the ecosystem as a whole crosses a threshold to a different state. For example, water yield from a watershed may increase dramatically after a fire kills all of the trees

in the watershed. Although the forest may have shifted to a long-lived grassland state as a result of the fire, the dramatic increase in water yield may be short lived, returning to prefire conditions in just a couple of years when the grasses become well established. Water managers would be interested in the NRV in this ecosystem property across the ecological threshold, and the temporary increase would simply be a part of that variation.

Plant diversity in the grasslands of North America's Great Plains is an ecosystem quality important to managers in this region, but its behavior is not well understood with respect to specific management practices or ecological thresholds. Consequently, NRV is a pragmatic approach for determining decision thresholds in this situation. In this chapter, we first outline the general process for determining the NRV of an ecosystem quality, then we use the plant diversity of Great Plains grasslands (GPG) to illustrate this process and, in so doing, provide specific values of these qualities and their NRV for GPG managers—information not available elsewhere. Finally, we discuss potential decision thresholds for specific GPG plant communities based on these values, and the implications of defining NRV in different ways.

A General Process for Quantifying Natural Range of Variation

Assuming that the community or ecosystem of interest is already well defined, the first step in describing NRV is to determine which attributes of that ecosystem will be used to describe that NRV. The attributes can be any of a wide variety of processes and properties, but they of course must be relevant to the management issue at hand and sufficient information about them must be available. A large part of the literature on NRV focuses on fire return intervals in forested systems and the resulting distribution of forest ages and types across the landscape (Bergeron et al. 2004; Carlson and Kurz 2007; Doyon et al. 2008; Mori and Lertzman 2011), but other attributes for which NRV has been quantified include spruce beetle irruption frequency and extent in Alaskan boreal forests (Sherriff et al. 2011), net ecosystem production in tropical forest (Sierra et al. 2007), and magnitude, frequency, and duration of river flows, as well as the spatial distribution and diversity of specific geomorphological forms, in the Colorado Front Range and Florida Everglades (Harwell 1997; Wohl 2011).

Second, appropriate spatial and temporal scales must be identified for the attributes of interest. Both must be broad enough that they allow for variation or heterogeneity in the ecosystem qualities of interest, but narrow enough that they encompass an ecosystem that is relatively consistent in terms of climatic, edaphic, topographic, and biogeographic conditions that are relevant to the management issue (Morgan et al. 1994). For example, differences in valley geometry, as well as variations in vegetation and hydrological flow regimes associated with elevation, translate into different NRVs among reaches within streams and among streams in mountainous regions (Wohl 2011). Bergeron et al. (2004) used dendrochronological techniques to estimate the mean fire intervals for mixed and coniferous boreal forests in eastern Canada prior to 1850, when European settlers began to impact the fire behavior of the region. The authors later decided that the length of time covered using these techniques (300–400 years) was too short to adequately capture the NRV given the

long life span of the tree species and communities that they were investigating, as well as the somewhat anomalous climate conditions of the 1770–1850 period (Cyr et al. 2009). Other issues to consider when choosing specific locations from which to gather NRV information include the location's history of management and other human influences, and the presence and abundance of exotic species (Landres et al. 1999).

Next, information must be compiled and translated into actual values of the attributes of interest. Methods used to do this depend on the choices made above and fall into five basic categories: study of historic records, analysis and interpretation of proxy records, modeling, space-for-time substitutions, and analysis of long-term monitoring data (Morgan et al. 1994; Egan and Howell 2001a). The last of these methods might be considered ideal, but consistently collected data over time periods long enough to address many NRV questions are rare. This is because the data-collection period must not only adequately cover the ecosystem of interest spatially, but also must be long relative to the return interval of external forces driving variability (disturbances, climatic fluctuations, etc.) and to the life span of the organisms of interest. Space-for-time substitutions can be used when a sufficiently large unaltered area, such as a large wilderness area, contains the range of conditions encompassed by the target ecosystem (Morgan et al. 1994). For example, current vegetation could be sampled in areas that have experienced various levels of grazing by native herbivores in order to describe the NRV of composition and productivity in a grassland ecosystem that evolved with these grazers. Dynamic simulation models that incorporate the effects of disturbances and stochastic fluctuations (as in weather) have been used to estimate the NRV of net ecosystem production, fire, and landscape dynamics, for example (Baker 1992; Sierra et al. 2007; Doyon et al. 2008). Models have the advantage of being able to cover a wide range of possible conditions that other methods may not, but they must be adequately calibrated to the location of interest to provide reasonable estimates. All three of these methods are subject to the same primary difficulty of finding an ecosystem minimally impacted by fire suppression, pollution, predator control, and other ecological disruptions caused by modern humans, to monitor, measure, or use to calibrate a model. Proxy methods that construct a chronology of past events based on pollen, microfossils, seeds, tree rings, fire scars, or lake sediments can avoid this problem, but they may not provide the temporal, spatial, or biological resolution desired (Swanson et al. 1994). Early land survey or forest reserve data may provide quantitative historical information (e.g., Graves 1899), but their use may be limited by lack of or unknown rigor, lack of detail, and their scarcity through time and space (Morgan et al. 1994). Finally, historical records such as photographs and explorers' journals can provide qualitative information where quantitative data cannot be obtained. For example, Higgins (1986) compiled and interpreted historical fire accounts from early European explorers' journals of their travels in the northern Great Plains to estimate fire frequency and seasonal distribution, but he pointed out the many limitations of this approach, including potential exaggeration by the journalists. Ideally, values of the attributes of interest will be derived using a combination of approaches so that the weaknesses of each approach are compensated for by the strengths of the other.

After values for the attributes of interest have been derived, the NRV of those attributes must be quantified. This can be done with a variety of metrics, the use

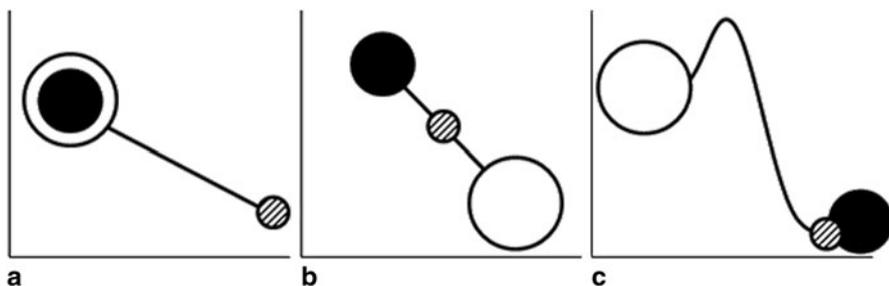


Fig. 8.1 Three potential relationships between natural range of variation (NRV; *open circle*), desired conditions (*filled circle*), and current conditions (*hatched circle*) and ease of path among them (*line*). **a** Desired conditions are within NRV; moving current conditions to either will require effort. **b** Desired conditions differ substantially from NRV, and moving current conditions to desired conditions will be difficult as the tendency is to move towards NRV. **c** A substantial ecological barrier (threshold) makes returning current conditions to within NRV extremely difficult, so desired conditions are in an alternate state

of which depends on the attributes of interest. Mean, median, standard deviation, percentiles, skewness, confidence intervals, and range describe an expected value and the magnitude and shape of the variation around that value. The coefficient of variation (CV; standard deviation divided by mean) is useful for describing the relative magnitude of fluctuations in an attribute through time, and frequency quantifies the rate of recurrence of an event type or ecosystem state. Mean and 95 % confidence intervals appear to be popular metrics for describing NRV (Bergeron et al. 2004; Sierra et al. 2007; Doyon et al. 2008; Cyr et al. 2009), but the full range of measured values is also sometimes used (Carlson and Kurz 2007; Sherriff et al. 2011). Although the central limit theorem ensures that the distribution of the mean of a large number of samples from any population will generally approximate a normal distribution, this does not mean that a given ecological variable will have a normal distribution. Thus, caution should be exercised when using parameters describing a normal distribution (mean, standard deviation) to describe the NRV of an ecological variable. Consequently, as with any quantitative data, it is always wise to perform a variety of exploratory data analyses to understand the shape of the data's distribution (Ellison 2001); this shape may itself be a useful means for describing the NRV (Landres et al. 1999).

Once the NRV is quantified, it is used for its intended purpose, which is usually to evaluate current conditions and determine desired conditions (Fig. 8.1). Desired conditions may be a subset of the NRV if parts of the NRV are not socially acceptable (e.g., intense, stand-replacing fires near urban areas) or if the full NRV is no longer possible due to land development, climate change, extinction, etc. (Fig. 8.1a; Swanson et al. 1994; National Park Service 2009; Thompson et al. 2009; Unnasch et al. 2009; Duncan et al. 2010). Desired conditions that differ substantially from the NRV for the former reason but not the latter may be difficult to attain or maintain without substantial, direct management (Fig. 8.1b). On the other hand, if an ecological threshold has been crossed, current conditions may be substantially outside the system's NRV. This situation may warrant setting the desired conditions outside the

NRV because conditions within the NRV are not feasibly attainable (Fig. 8.1c). For the rest of our discussion, we will focus on the scenario in Fig. 8.1a, where desired conditions lie wholly within the NRV.

Process for Great Plains Grasslands Plant Diversity Natural Range of Variation

Focal Ecosystem

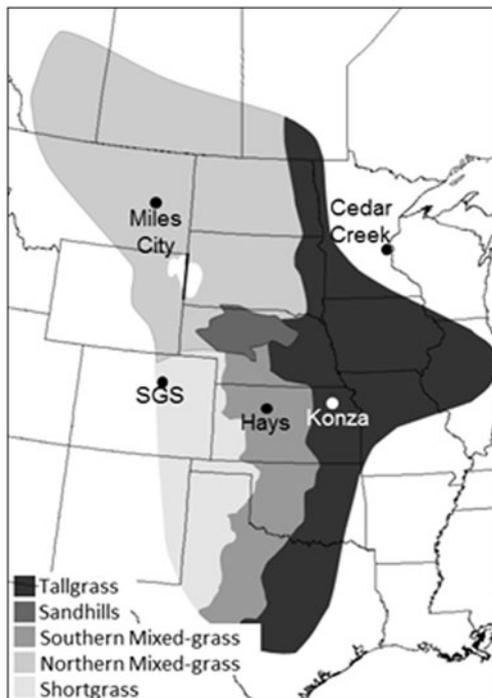
GPG cover an area of approximately 2 million km² in mid-continental North America. Vegetation biomass is dominated by grasses, but forbs generally provide much of the diversity. Temperature and precipitation gradients across the region result in a general west-to-east increase in productivity and plant species richness (Teeri and Stowe 1976; Risser et al. 1981) and a gradient of broad grassland types (Lauenroth et al. 1999; Fig. 8.2). Local variations in soils and topography yield a variety of plant assemblages at finer spatial scales. Temporal climate variability is high throughout the region, more so than in the remainder of North America east of the Rocky Mountains (Borchert 1950). These climatic forces, as well as periodic fire and herbivory by large ungulates (bison, elk, and pronghorn), insects, and prairie dogs, shaped the evolution of GPG (Axelrod 1985; Anderson 2006). Today, major factors affecting this highly endangered ecosystem include land use patterns, exotic and invasive species, atmospheric nitrogen deposition, altered fire and grazing regimes, and climate change (Samson and Knopf 1994), and most of these have been shown to affect plant diversity in the region (Symstad and Jonas 2011).

The term “Great Plains grasslands” encompasses far too broad an area for meaningful characterization of NRV of any ecosystem characteristic, but this area hosts at least 19 National Park Service (NPS) units where plant diversity has been identified as an important measure of ecosystem health (DeBacker et al. 2004; Manier et al. 2011; Symstad et al. 2011), as well as a wide variety of other federal, state, and private lands where native grasslands are being managed and restored. In order to serve this broad audience but also provide meaningful values, we present NRV information for one or two sites from four of the five major grassland types in the Great Plains (Fig. 8.2), separated by topoedaphic class within these sites when appropriate.

Attributes of Interest

We focus on plant diversity for three reasons. First, the NPS mission is to preserve and protect the landscapes and organisms within its holdings for the enjoyment of future generations. Consequently, maintaining or restoring diversity is increasingly becoming an explicit management goal of many NPS units. Second, a large body of research investigating the relationship between biodiversity and ecosystem functioning over the past 15 years has shown that greater plant diversity on average results not

Fig. 8.2 Major grassland types of North America's Great Plains (after Lauenroth et al. 1999), and locations of datasets described in Table 8.1



only in higher production, but also in more stable production (Tilman 2001; Hooper et al. 2005; Balvanera et al. 2006; Cardinale et al. 2006, 2007; Fargione et al. 2007; Schmid et al. 2009; Isbell and Wilsey 2011), and that maintaining high levels of multiple ecosystem functions (e.g., nutrient retention and belowground carbon storage in addition to aboveground production) requires more species than maintaining a high level of just one ecosystem function (Hector and Bagchi 2007; Zavaleta et al. 2010). Consequently, Briske et al. (2006) proposed species loss as one category of threshold that rangelands cross when progressing from a desirable state to an undesirable state. Little information to evaluate this suggestion is available, however. Thus, our third reason for focusing on plant diversity is to begin filling that information gap. The Natural Resource Conservation Service's nationwide effort to describe the dynamics of rangeland (including GPG) vegetation in response to various management practices provides a wealth of information on the variability of dominant plant species (Bestelmeyer et al. 2003, 2009; see Bowker et al. (Chap. 7) for a thorough description of this process), but provides no information on plant diversity.

We use two metrics of plant diversity—species richness and species evenness (hereafter richness and evenness). Richness is the number of species in a given area (i.e., those counted in a sample of fixed area), whereas evenness is a metric quantifying the relative abundance of species in that area. We use the Shannon evenness index, calculated as $(-\sum p_i \ln p_i) / \ln S$, where p_i is the proportional abundance of species i , and S is the total number of species (i.e., richness; Magurran 1988). Evenness ranges from 0 to 1, with values near 0 indicating greater dominance by a single

species and values near 1 indicating nearly equal abundance of all species present. We use both of these metrics because they are expected to respond to ecosystem stressors differently. Richness will be more sensitive to stressors that cause the loss of only relatively rare species, whereas a stressor that causes significant shifts in the way resources are partitioned among species could affect evenness without substantially affecting richness. Because of the different information contained in these two metrics, we do *not* use any of the indices that combine richness and diversity into one value and are usually referred to as diversity indices.

Spatial and Temporal Scale

Although plant diversity is an important descriptor of a plant community, any metric describing it is complicated by its sensitivity to the area over which it is sampled. Consequently, we focus on richness and evenness at the —quadrat or transect scale (see Table 8.1 for sizes and explanation of scale chosen for each site) because it is the scale most comparable among management units and between current and reference conditions. In addition, because annual fluctuations in climate are significant drivers in GPG vegetation, we felt it was important to characterize variability with a high temporal resolution—an annual time step.

Information Sources and Approach

Given these attributes, metrics, and goals, the best method for describing NRV in GPG vegetation was analysis of long-term monitoring data. We found six datasets that have sufficient temporal length (> 10 years) and resolution (annual), have enough detail (abundance of individual species recorded in a fixed location) to calculate richness and evenness, and are from relatively unimpacted ecosystems (e.g., fire not excluded, low exotic species abundance). Data come from five sites: the Shortgrass Steppe (SGS), Konza Prairie (Konza), and Cedar Creek (Cedar Creek) long-term ecological research stations, Fort Hays State University (Hays), and Fort Keogh Livestock and Range Research Laboratory (Miles City). Two datasets (Konza FRI and Konza Grazed), from two separate experiments at Konza, were kept separate in our analyses. Table 8.1 describes these datasets, two of which are historic and four of which are modern. We refined the datasets to include only quadrats (transects for Konza datasets; Table 8.1) for which data were reported for at least 80 % of the time series. For all datasets except Cedar Creek, exotic species occur in up to 68 % of sample units, but, averaged over all sample units in each dataset, they comprise < 6 % of total richness and < 5 % of plant cover/density. Exotics are more abundant in the Cedar Creek datasets. Consequently, for this dataset, we only included plots that never had > 25 % exotic species cover. Each dataset was accompanied by weather data from a nearby (<12 km) meteorological station for the period during which the vegetation data were collected.

Table 8.1 Datasets used to assess natural range of variability (NRV) in Great Plains grasslands (GPG)

Name	Location	Subset (<i>n</i> = sample size)	Period of record	Data	Source, reference
SGS	Shortgrass Steppe LTER North-central Colorado Loamy and sandy plains Shortgrass prairie Annual precip: 348 mm Mean annual temp: 9.0 °C	Grazing exclosure <i>n</i> = 12 ^a Moderate summer cattle grazing <i>n</i> = 12 ^a	1998–2006 1998–2006	Number of individuals for each species counted in 1-m ² quadrat	Control treatment of <i>Bouteloua gracilis</i> removal experiment http://sgs.cnr.colostate.edu/dataset_view.aspx?id=BOGRRRmviDnsty (accessed 27 Sept 2011) (Munson and Lauenroth 2009)
Hays	Fort Hays State Univ. Central Kansas Loamy and limy rolling hills Southern mixed-grass prairie Annual precip: 577 mm Mean annual temp: 12.1 °C	Big bluestem: swales <i>n</i> = 3 or 4 Little bluestem: shallow limestone on hill brows and slopes <i>n</i> = 8–12 Ecotone between little bluestem and shortgrass <i>n</i> = 6 (1933–1942) <i>n</i> = 14 (1942–1972) Shortgrass: deep soils on level uplands <i>n</i> = 4–6 Grazed shortgrass: deep soils on level uplands <i>n</i> = 8–15	1932–1968, 1970–1972 1932–1972 1933–1972 1932–1972 1935–1972	Basal cover of each species in 1-m ² quadrat mapped using pantograph	Historic rangeland monitoring data digitized by Adler et al. (2007)

Table 8.1 (continued)

Name	Location	Subset (<i>n</i> = sample size)	Period of record	Data	Source, reference
Miles City	Fort Keogh Livestock and Range Research Lab Eastern Montana Silty and clayey ecological sites Northern mixed-grass prairie Annual precip: 305 mm Mean annual temp: 8.2 °C	<i>Light grazing</i> (7.9 ha • AUM^{-1}) <i>n</i> = 7–13 <i>Moderate grazing</i> (6.2 ha • AUM^{-1}) <i>n</i> = 11–18 <i>Heavy grazing</i> (4.7 ha • AUM^{-1}) <i>n</i> = 8–11	1933–1945 1933–1945 1933–1945	Basal cover or stem count of each perennial species mapped in 1-m ² quadrat using pantograph; number of individuals in same 1-m ² quadrat recorded for annual species ^b	Historic rangeland monitoring data digitized by Anderson et al. (2011)
Cedar Creek	Cedar Creek LTER East-central Minnesota Well-drained sandy plains Sand tallgrass prairie/oak savanna Annual precip: 804 mm Mean annual temp: 6.7 °C	Nitrogen addition (<i>N</i>) = 0 g/m ² (<i>n</i> = 10) ^c <i>N</i> = 1.02, 2.04, 3.40, 5.44, 9.52, 17.0, or 27.2 g/m ² (<i>n</i> = 5 each)	1982–2004 1982–2004	Aboveground biomass: above-ground biomass clipped, dried and weighed by species at peak biomass in 0.1 × 3 m strips alternating location within each 4 m × 4 m plot	Field D of Experiment 001 (long-term nitrogen deposition) http://www.lter.umn.edu/research/data/ (accessed 20 Sept 2011) (Tilman 1987)
Konza FRI	Konza Prairie LTER Eastern Kansas (Flint Hills) Cherty silt loam (upper slope), silty clay loam (lower slope) Tallgrass prairie	<i>Upper</i> (<i>n</i> = 4), <i>mid</i> (<i>n</i> = 4), or <i>lower</i> (<i>n</i> = 4) slope burned every year	1983–2007 (<i>upper and lower</i>); 1991–1992, 1997–2001, 2006 (<i>mid</i>)	Percent canopy cover (modified Daubenmire cover classes) recorded by species in five 10-m ² quadrats along 50-m transect ^d	Ungrazed watersheds of dataset PVC02 http://www.konza.ksu.edu/KNZ/pages/data/Knzdsdetail.aspx?datasetCode=PVC02 (accessed 14 July 2008) (Collins et al. 1995; Collins 2000)

Table 8.1 (continued)

Name	Location	Subset (<i>n</i> = sample size)	Period of record	Data	Source, reference
	Annual precip: 824 mm Mean annual temp: 13.2 °C	Upper (<i>n</i> = 4 or 8), mid (<i>n</i> = 4 or 8), or lower (<i>n</i> = 4) slope burned every 4 years <i>Upper</i> (<i>n</i> = 4), <i>mid</i> (<i>n</i> = 4) or <i>lower</i> (<i>n</i> = 4) slope burned every 20 years	1983–2007 (upper and lower); 1991–2011, 2006 (mid) 1983–2007 (<i>upper and lower</i>); 1991–2011, 2006 (<i>mid</i>)	Evenness calculated only after 1988 because cover estimation methods changed in 1989	
Konza Grazed	Konza Prairie LTER Eastern Kansas (Flint Hills) Cherty silt loam (upper slope), silty clay loam (lower slope) Tallgrass prairie Annual precip: 816 mm Mean annual temp: 13.0 °C	<i>Moderate summer bison grazing on upper</i> (<i>n</i> = 8), <i>mid</i> (<i>n</i> = 4), or <i>lower</i> (<i>n</i> = 8) slope burned every year <i>Moderate summer bison grazing on upper</i> (<i>n</i> = 8), <i>mid</i> (<i>n</i> = 8), or <i>lower</i> (<i>n</i> = 8) slope burned every 4 years <i>Moderate summer bison grazing on upper</i> (<i>n</i> = 8), <i>mid</i> (<i>n</i> = 8), or <i>lower</i> (<i>n</i> = 8) slope burned every 20 years	1994–2007 (<i>upper and lower</i>); 1997–2007 (<i>mid</i>) 1994–2007 (all) 1994–2007 (<i>all</i>)	Percent canopy cover (modified Daubenmire cover classes) recorded by species in five 10-m ² quadrats along 50-m transect ^d	Bison-grazed watersheds of dataset PVC02 http://www.konza.ksu.edu/KNZ/pages/data/KNZsdetail.aspx?datasetCode=PVC02 (accessed 14 July 2008) (Hartnett et al. 1997; Towne et al. 2005)

In the subset column, treatments considered to most closely approximate reference conditions are in normal font; management practices that deviate from approximate reference are given in *italics*

^a Species richness and evenness did not differ among subsets through time (repeated measures ANOVA subset and subset × year effects *p* > 0.32)

^b Because methods used to measure abundance varied among species (and within species among years), evenness could not be calculated

^c Combination of treatments A and I (Tilman 1987), which did not differ in species richness and evenness through time (*p* > 0.10)

^d Data analyzed at transect level because quadrats were not labeled consistently across years

Quantifying NRV

For each dataset, we calculated richness and evenness for each quadrat (or transect for Konza datasets) in each year (including all species), then tested for significant differences in richness and evenness among community types (Hays), treatments (SGS, Miles City, Cedar Creek), or soil type \times treatment combinations (Konza FRI and Konza Grazed) with repeated measures ANOVAs. These effects or their interaction with each year were significant ($p < 0.05$) for all but one dataset (SGS). Thus, each community type, treatment, or soil type \times treatment was treated separately for all datasets except SGS, in which all subsequent calculations combined the two grazing treatments into a single time series. We calculated annual richness and evenness means and 95 % confidence interval of those means for each community type/treatment/soil \times treatment, as well as the median and 10th, 25th, 75th, and 90th percentiles and full range of each response variable over the entire time series for a single reference treatment (where applicable; see Table 8.1). As a measure of temporal variability, we calculated the CV in richness and evenness through time for each quadrat/transect.

Since species richness or evenness fluctuations may be related to fluctuations in precipitation via individual species' response to moisture, we also quantified temporal variability of precipitation as the CV of mean annual precipitation over the period in which vegetation data were collected. Interannual fluctuations in GPG aboveground net primary production are also considerable and have been characterized much more fully than fluctuations in species richness or evenness (Webb et al. 1978, 1983; Sala et al. 1988; Smart et al. 2007). To put the variability of species richness and evenness in the context of variability of this other important GPG attribute, we calculated the CV of total density, cover, or biomass (measure varies among datasets; see Table 8.1) through time for each quadrat or transect.

Variation of Plant Species Richness and Evenness in Great Plains Grasslands

Median species richness in 1-m² quadrats varies from 4 to 12, and evenness varies from 0.34 to 0.68, in western GPG (SGS, Hays, and Miles City; Figs. 8.3–8.5). In the more productive and diverse eastern GPG, median species richness is 14 in just 0.3 m² in the sand savanna (Cedar Creek; Fig. 8.6a), and 37–54 species in five 10-m² quadrats in the Flint Hills of Kansas (Konza; Fig. 8.7a–c, g–i); median evenness was similar between the sites, ranging from 0.623 to 0.675 (Figs. 8.6b, 8.7d–f, j–l). The low evenness values at Hays (Fig. 8.4, *right*) compared to the other sites may be due to the way that species abundance was measured (basal cover vs. density or foliar cover) rather than an inherent difference in structure of the plant community.

Temporal variability of species richness in these datasets is fairly consistent across the wide variety of conditions occurring in shortgrass prairie in Colorado (SGS) to tallgrass sand savanna in Minnesota (Cedar Creek), with richness CVs in the

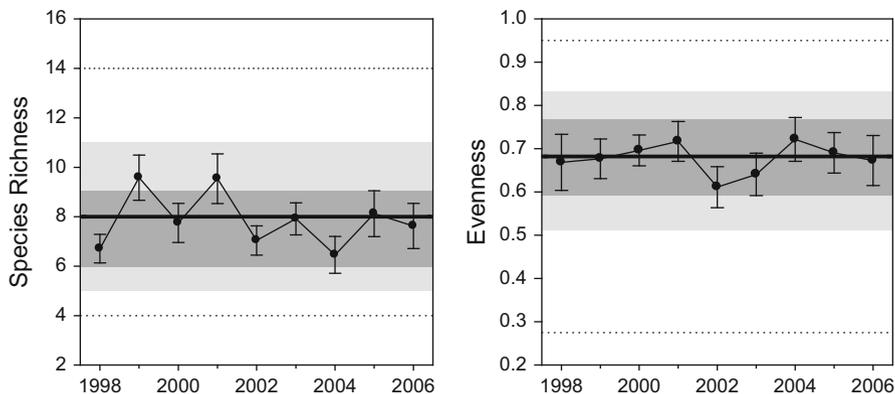


Fig. 8.3 Mean (\pm 95 % CI) annual species richness (*left*) and evenness (*right*) in 1-m² quadrats in northeastern Colorado shortgrass prairie (SGS dataset). *Bands* indicate 25–75th (*darker gray*) and 10–90th (*lighter gray*) percentile range of all values measured in indicated time period, and *dotted lines* indicate the full range of these values. The *thick horizontal line* is the long-term median of these values

0.20–0.45 range (Table 8.2). Flint Hills tallgrass prairie (Konza) shows much lower richness CVs (< 0.20), but this is likely due to the much larger area covered by each sample. The chances of one or a few species winking in or out from one year to the next are presumably much higher in a small quadrat than in the 50-m² area sampled for the Konza datasets. Higher species richness CVs seem to be related more to whether a time series includes the 1930s Dust Bowl period of extreme drought in this region rather than to the length of the time series. Comparing richness CVs from SGS and Cedar Creek (Dust Bowl not included) to those of Hays and Miles City (Dust Bowl included), versus comparing SGS and Miles City (< 15 years) to Cedar Creek and Hays (\geq 25 years), illustrates this point (Table 8.2). Temporal variability of evenness spans a larger range among the time series than does species richness variability, but evenness CV is not consistently greater than that of richness at a given site.

Temporal variability of species richness in these datasets is consistently lower than that of production (Table 8.2) suggesting that this may be true across a wider range of locations than those investigated here. In contrast, temporal variability of evenness relative to that of production is inconsistent within and across sites, as is the variability of richness or evenness relative to precipitation. The latter indicates that, although GPG production is generally related to temporal variations in precipitation (Webb et al. 1978, 1983; Sala et al. 1988; Smart et al. 2007), the same is not true for GPG diversity. Indeed, analyses investigating the relationship between plant species richness and a variety of weather variables in GPG suggests that there is little consistency in these relationships across sites or among management treatments within sites (Jonas et al. in revision). It is important to note, however, that temporal variability in richness and evenness is frequently of similar magnitude to differences in the metrics among management treatments (e.g., fire; Fig. 8.7d–f vs. Fig. 8.8b) or

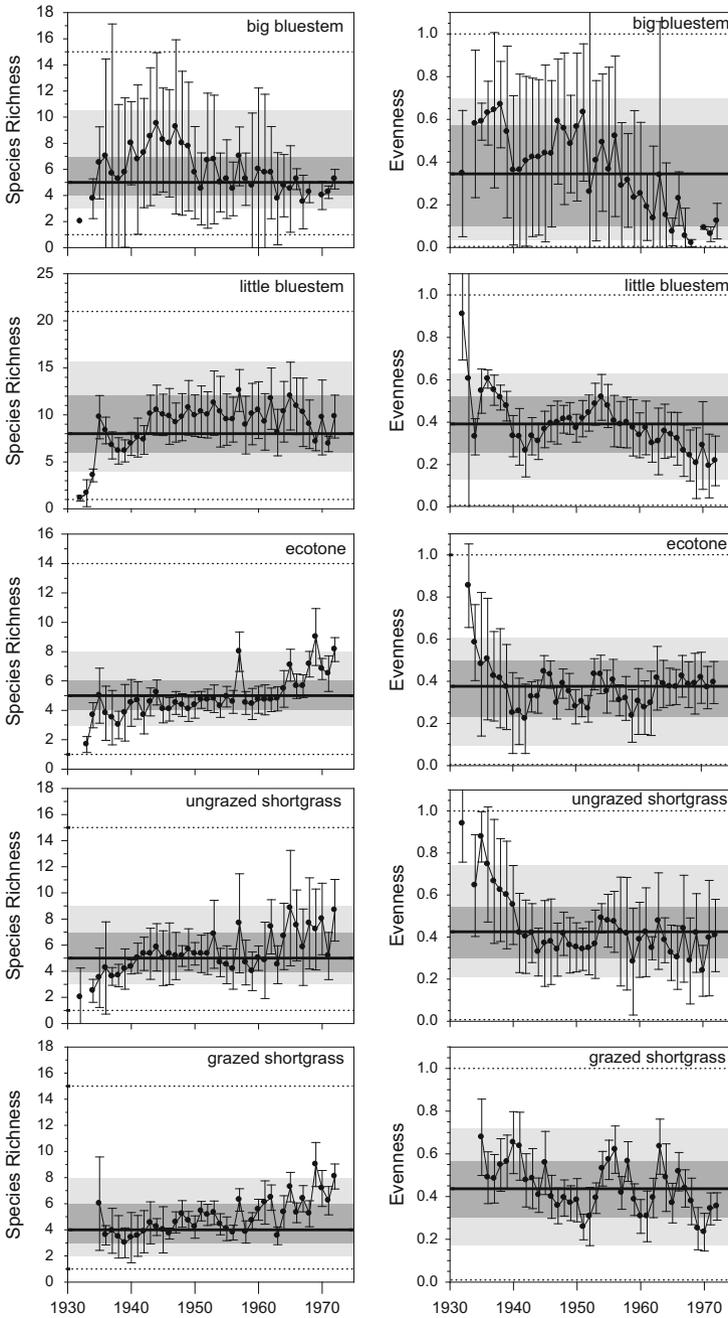


Fig. 8.4 Mean ($\pm 95\%$ CI) annual species richness (*left*) and evenness (*right*) in 1-m² quadrats in five vegetation types in central Kansas mixed-grass prairie (Hays dataset). Shading and lines as in Fig. 8.3

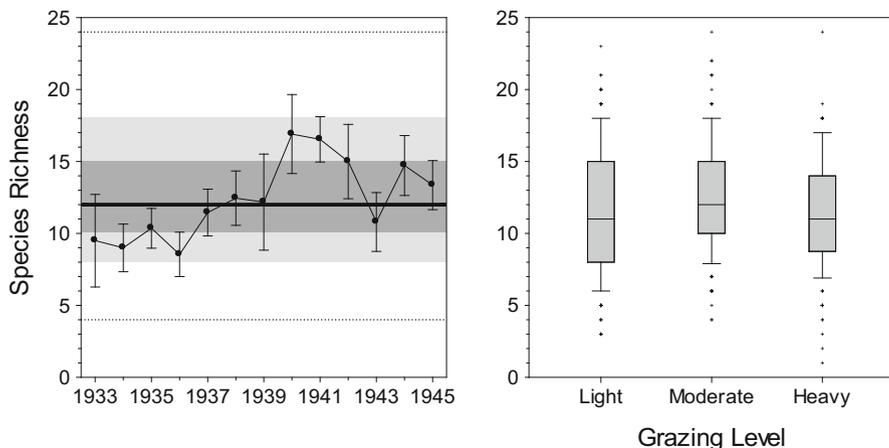


Fig. 8.5 (Left) Mean (\pm 95% CI) annual species richness in 1-m² quadrats in moderately grazed mixed-grass prairie in eastern Montana (Miles City dataset). Shading and lines as in Fig. 8.3. (Right) Box-whisker diagrams for light, moderate, and heavy grazing treatments at the same location and over the same time period depicted at left. For each treatment, the median (*central line*), middle quartiles (*box*), 10th and 90th percentiles (*whiskers*), and outlying values (+ 's) are shown

experimental treatments simulating anthropogenic stresses (e.g., nitrogen deposition; Fig. 8.6b vs. Fig. 8.6d). This “noise” that makes detecting effects of these factors on GPG difficult has been noted previously by other authors (Gibson and Hulbert 1987; Biondini et al. 1989; Coppedge et al. 1998; Wienk et al. 2009).

Where Should the Decision Threshold Be?

Possible ranges of plant species richness and evenness that might be considered NRVs for a variety of GPG communities are illustrated in Figs. 8.3–8.7. By definition, the range spanning the 25–75th percentiles (“interquartile” range; dark gray band in Figs. 8.3–8.7) includes half of the values measured, whereas the 10–90th percentile range (light gray band) includes 80% of them. In most cases, the latter range is substantially larger than the former, indicating substantially different deviations from the central tendency that would be needed to spur a change in management activity if the decision threshold were simply the outside bound of the NRV. For example, the declining values of species richness in fertilized plots at Cedar Creek (Fig. 8.6a) could prompt action in 1985 if the decision threshold were determined by the interquartile range, but they would not garner attention until 1988, or possibly even 1996, if the decision threshold were based on the wider 10–90th percentile range. And, of course, there would be no action at all if the decision threshold was based on the full range of values. Basing NRVs and decision thresholds on this full range is particularly problematic for Hays, the longest dataset and one that began during the Dust Bowl,

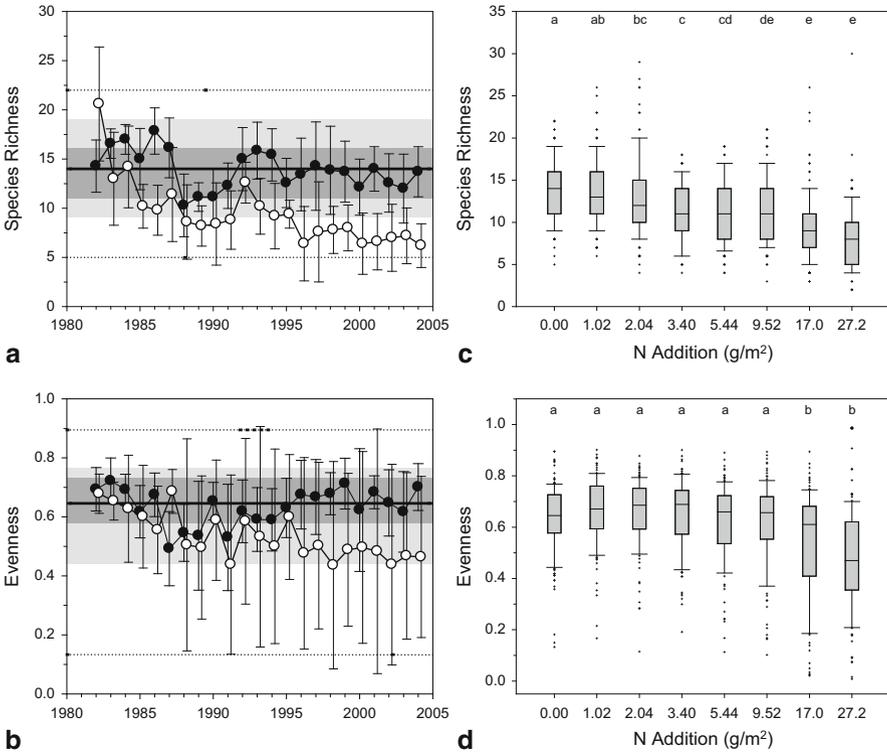


Fig. 8.6 **a, b** Mean (\pm 95 % CI) annual species richness (**a**) and evenness (**b**) in 0.3-m² quadrats in unfertilized (reference condition; *black circles*) and fertilized (17.0 g nitrogen/m², *white circles*) sand savanna in east-central Minnesota (Cedar Creek dataset). Fertilized time series are offset slightly for clarity. Shading and lines as in Fig. 8.3. **c, d** Box-whisker diagrams for nitrogen (N) addition treatments at the same location and over the same time period depicted in (**a**) and (**b**). For each treatment, the median (*central line*), middle quartiles (*box*), 10th and 90th percentiles (*whiskers*), and outlying values (*+*'s) are shown. Lower-case letters above boxes indicate significant differences among treatments ($p < 0.05$)

because the range of evenness values experienced by the system essentially equals the full range of values mathematically possible for this index.

A single location's species richness value falling outside of the range chosen as the NRV under current conditions would generally not warrant the management action prescribed by the decision threshold. Decisions would be based on the mean or median of the sample frame and the confidence in that estimate. A single year's crossing out of the NRV also might not warrant immediate action. For example, if we say that the NRVs in Fig. 8.6a are independent of the time series shown therein, the drop in mean species richness of the unfertilized plant community at Cedar Creek below the interquartile range in 1988 might not spur action because richness returns to within this range the next year and stays there for the duration of the monitoring. Thus, a decision threshold might require that the metric of interest show a consistent trend of

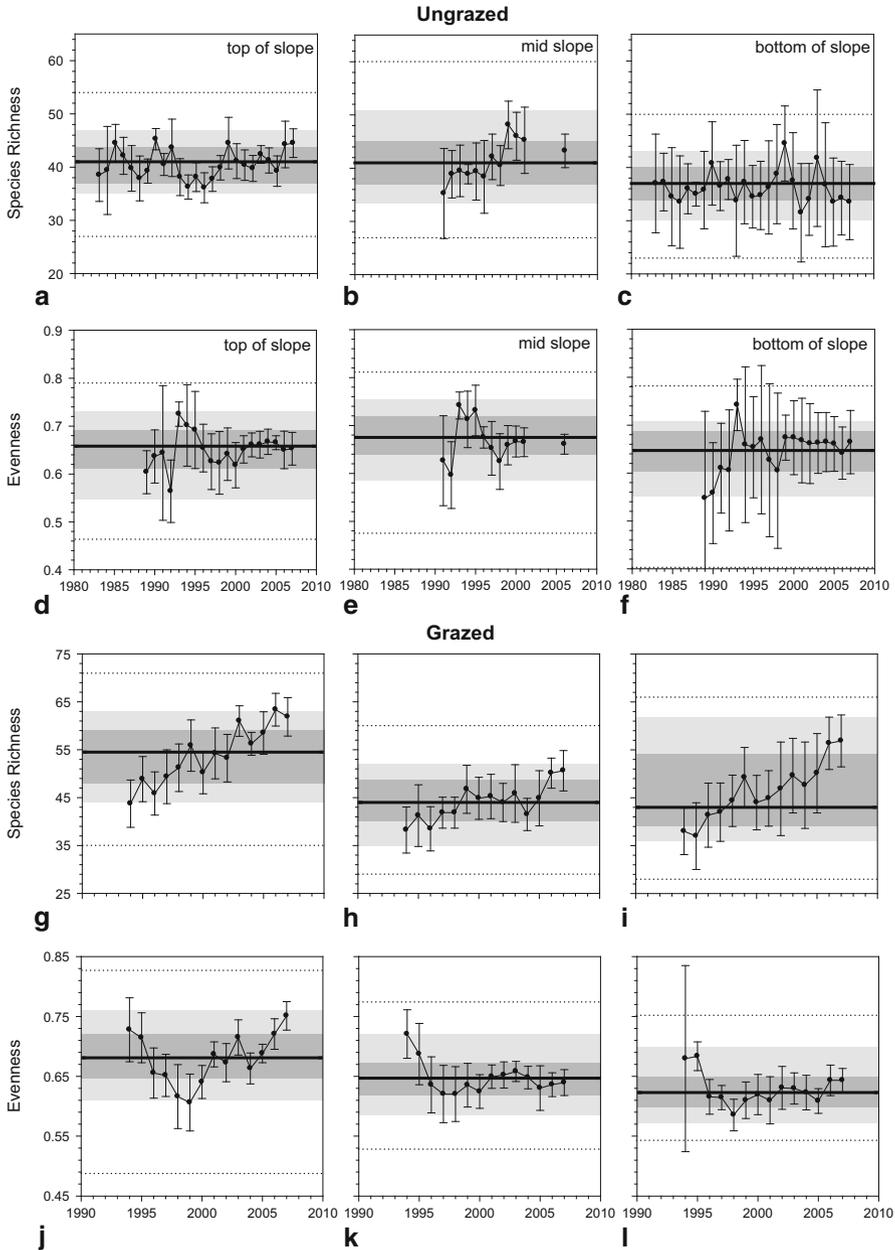


Fig. 8.7 Mean ($\pm 95\%$ CI) annual species richness and evenness for five 10-m^2 quadrats in quadrennially burned, ungrazed (**a–f**) and grazed (**g–l**) tallgrass prairie in three different topographic positions/soil types in eastern Kansas (**a–f**, Konza FRI dataset; **g–l**, Konza Grazed dataset). *Shading and lines* as in Fig. 8.3

Table 8.2 Temporal variability of plant species richness, evenness, and production in reference (*plain font*) or alternative reference (*italics*) conditions for datasets described in Table 8.1

Dataset	Prairie type	Subset	CV of species richness	CV of evenness	CV of "production" (total density, cover, or biomass)	CV of precipitation	
SGS	Shortgrass	Grazed and ungrazed combined	0.231 (0.112–0.395)	0.677 (0.275–0.950)	0.502 (0.237–0.900)	0.333	
Hays	Mixed-grass	Big bluestem	0.358 (0.326–0.380)	0.696 (0.486–0.838)	0.477 (0.369–0.563)	0.258	
		Little bluestem	0.319 (0.228–0.423)	0.493 (0.235–0.693)	0.404 (0.309–0.532)		
		Little bluestem-shortgrass ecotone	0.382 (0.219–0.536)	0.482 (0.227–0.846)	0.444 (0.327–0.580)		
		Shortgrass	0.408 (0.292–0.490)	0.469 (0.374–0.755)	0.571 (0.488–0.650)		
		Shortgrass (grazed)	0.429 (0.291–0.545)	0.448 (0.346–0.649)	0.489 (0.405–0.612)		
Miles City	Mixed-grass	Low grazing (7.9 ha • AUM ⁻¹)	0.360 (0.207–0.614)	Could not be calculated	0.331		
		Medium grazing (6.2 ha • AUM ⁻¹)	0.282 (0.186–0.436)				
		High grazing (4.7 ha • AUM ⁻¹)	0.330 (0.239–0.528)				
Cedar Creek	Sand tallgrass		0.233 (0.195–0.278)	0.183 (0.102–0.326)	0.619 (0.405–0.882)	0.210	
Konza FRI	Tallgrass	Annually burned upland	0.088 (0.074–0.104)	0.105 (0.084–0.120)	0.195 (0.139–0.235)	0.234	
		Annually burned slope	0.060 (0.039–0.102)	0.181 (0.132–0.218)	0.129 (0.097–0.196)		
		Annually burned lowland	0.077 (0.069–0.088)	0.107 (0.101–0.115)	0.175 (0.144–0.255)		
		Quadrennially burned upland	0.106 (0.068–0.131)	0.080 (0.060–0.105)	0.191 (0.155–0.233)		
		Quadrennially burned slope	0.131 (0.078–0.178)	0.087 (0.036–0.113)	0.195 (0.120–0.275)		
		Quadrennially burned lowland	0.112 (0.094–0.140)	0.099 (0.063–0.150)	0.270 (0.212–0.351)		
Konza Grazed	Tallgrass	Grazed annually burned upland	0.117 (0.086–0.143)	0.073 (0.057–0.092)	0.240 (0.187–0.328)	0.219	
		Grazed annually burned slope	0.084 (0.062–0.103)	0.054 (0.037–0.076)	0.232 (0.182–0.300)		
		Grazed annually burned lowland	0.199 (0.163–0.250)	0.081 (0.049–0.097)	0.223 (0.167–0.299)		
		Grazed quadrennially burned upland	0.127 (0.108–0.156)	0.076 (0.051–0.140)	0.187 (0.115–0.288)		
		Grazed quadrennially burned slope	0.110 (0.070–0.147)	0.060 (0.041–0.090)	0.214 (0.134–0.337)		
		Grazed quadrennially burned lowland	0.160 (0.071–0.221)	0.064 (0.048–0.085)	0.233 (0.155–0.291)		

Values shown are the mean (min–max) coefficient of variation (CV) for transects (Konza) or quadrats over the time described for the dataset in Table 8.1. For comparison, CV of precipitation over that time period is also given

deviating from the NRV. Taking action also requires understanding the reason for the departure. In the Cedar Creek example, the precipitous drop in richness was caused by a severe drought (Tilman and El Haddi 1992), a natural environmental driver usually requiring no management intervention. On the other hand, if the departure from NRV were linked to a fertilizer spill, remedial action should be taken.

How long to wait, though, will depend on the relative costs and benefits of acting when the system can actually recover on its own versus being too slow in taking action so that the system crosses into an undesirable state from which it cannot recover. These costs and benefits are formally codified in a utility function (Martin et al. 2009; Nichols et al. Chap. 2), which also incorporates knowledge about the ecosystem's response to specific management actions with respect to management objectives. Since utility functions are unique to each management situation and are relatively rare for vegetation management in natural areas, we do not address this issue. We emphasize, however, that using management thresholds and assessment points based simply on NRV is a reasonable first step towards constructing more rigorous decision-making models in GPG.

A judicious approach in this situation would be to designate the interquartile NRV as the bounds for instigating more attention, such as more detailed analyses of data (e.g., closer look at species composition, exotic species richness and abundance, or woody plant cover) or increasing the intensity of sampling (surveillance assessment points; Mitchell et al., Chap. 10), and to designate the broader 10–90th percentile NRV as the bounds to instigate a specific-management action (action assessment point). The rationale for having these two different assessment points is to avoid the cost (monetary and ecological) of initiating an action when unnecessary, such as when the system returns to the narrower NRV prior to reaching the action assessment point.

Some Notes About the Values We Present

Designating what constitutes the “reference” condition is far from straightforward in an ecosystem that does not lend itself to most historical reconstruction techniques (e.g., dendrochronology). Although there is uncertainty about the intensity, frequency, and spatial patterning of fire and grazing before European settlement in all of these systems, we are certain that the conditions maintained at the sites from which we obtained our data substantially diverged from presettlement conditions. For example, grazing at these sites, if it occurred at all, was much more regulated (timing and intensity) than what occurred when large herds of bison, elk, and pronghorn freely roamed the Great Plains, and there are known differences in behavior and dietary preferences between these native grazers and domestic cattle (Plumb and Dodd 1993; Hartnett et al. 1997; Towne et al. 2005). Prescribed fire, if it occurred at all, was also applied quite regularly and uniformly and during conditions that do not necessarily mimic those of presettlement times (Higgins 1986). Because it is impossible to return to presettlement fire and grazing regimes and undo landscape

fragmentation, atmospheric pollution (including greenhouse gas emissions), etc., the species richness and evenness values we present are reasonable alternatives.

Although we used only one “reference” condition to illustrate fluctuations in species richness and evenness through time (Figs. 8.3–8.7), we acknowledge that others may disagree with those choices by presenting summary information on temporal variability (Table 8.2) and overall variation (Figs. 8.5, 8.8) for conditions that could also be considered reference. For example, although the assumed fire return interval in presettlement tallgrass prairie is 3–5 years (Knapp et al. 1998; hence our using the 4-year fire return interval as the reference condition for Konza datasets), shrub cover has steadily increased under these conditions at Konza, whether grazed or not (Heisler et al. 2003; Briggs et al. 2005; Ratajczak et al. 2011), indicating the vegetation is not in reference condition despite the maintenance of the historical fire frequency. Indeed, shrub cover at Konza has increased slightly even under annual burning, indicating that management more aggressive than the historical fire regime may not be able to attain or maintain vegetation within the NRV in the face of changing atmospheric and herbivory conditions (Briggs et al. 2005).

We also acknowledge that some datasets probably do not adequately describe NRV for certain conditions. In particular, species richness has continuously increased since bison grazing was initiated in 1994 in the Konza datasets (Fig. 8.7g–i), indicating that the system has not yet reached equilibrium with the new conditions. Similarly, the Miles City dataset, begun in the Dust Bowl, may not be long enough to capture the full recovery of the system from this severe drought (Albertson and Weaver 1944; Adler and Levine 2007; i.e., compare Figs. 8.4 and 8.7).

The datasets we used cover only a small subset of the many grassland-vegetation assemblages that occur across the Great Plains. However, the values we derived for NRVs (interquartile and 10–90th percentile ranges) provide a starting point for managers at other sites. For example, species richness in a native prairie unit at Fort Union Trading Post National Historical Site in western North Dakota is well within the center of the interquartile range for Miles City. This position is consistent with other aspects of the vegetation at Fort Union that suggest that it is in good condition (Symstad 2011). On the other hand, the mixed-grass prairie at Scotts Bluff National Monument in western Nebraska has a substantial amount of invasive, annual brome (*Bromus* spp.) grasses, suggesting poor condition. Species richness there is well below the 10th percentile of Miles City mixed-grass prairie and near the 25th percentile for the mixed-grass communities at Hays (Symstad 2005). When determining whether the values presented here are relevant for other sites, managers would benefit from a short term but spatially extensive sampling of one or more reference sites relevant to their location. Given the paucity of long-term monitoring in GPG vegetation, however, we believe the temporal variability information we present (CVs in Table 8.2) is likely to be the best available.

Unfortunately, the natural variability of these metrics through time may make detecting trends towards undesirable changes in GPG vegetation difficult. For example, Collins et al. demonstrated that annual spring burning of tallgrass prairie in the Flint Hills of Kansas is known to lead to statistically significantly lower species richness compared to areas burned every 3–4 years (Collins et al. 1995; Collins 2000;

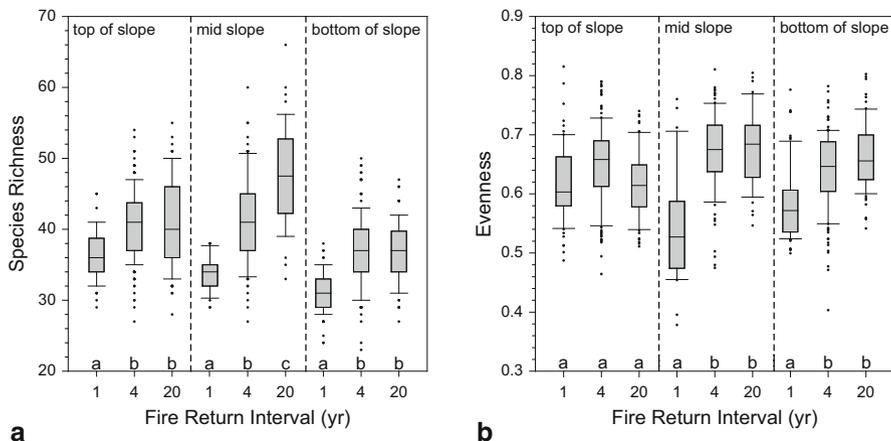


Fig. 8.8 Box-whisker plots of species richness (a) and evenness (b) values from five 10-m² quadrats for three fire return interval treatments in three topographic positions/soil types in ungrazed, eastern Kansas tallgrass prairie, 1983–2007 (richness) or 1989–2007 (evenness) (Konza FRI dataset). For each treatment × topographic position combination, the median (*central line*), middle quartiles (*box*), 10th and 90th percentiles (*whiskers*), and outlying values (+ 's) are shown. *Lower-case letters* below boxes indicate significant differences among treatments within topographic position ($p < 0.05$)

Fig. 8.8a). In the Konza FRI dataset, the difference between annual and quadrennial burning is reflected by the fact that the median richness of annually burned prairie is below the 25th percentile for the quadrennially burned (reference condition) in each of the three slope positions prairie (Fig. 8.8a). On the other hand, even fairly low levels of nitrogen fertilization have been shown to significantly reduce species richness at Cedar Creek (Tilman 1987; Clark and Tilman 2008; Fig. 8.6c), but the median value of richness in significantly impacted plots (2.04 and 3.40 g N/m² added per year) is well within the interquartile range of richness for the unfertilized plots (Fig. 8.6c). In this case, the experimental evidence supports setting surveillance-assessment points within a narrower range than the interquartile based on temporal variability, but action assessment points/decision thresholds would need to be tempered by the fact that a severe drought (in 1987–1988) drove species richness and evenness well outside the interquartile range (Fig. 8.6a, b).

Conclusions

In ecosystems exhibiting a wide range of natural variability, identifying ecological or decision thresholds can be challenging. Employing the NRV concept to describe attributes of interest based on long-term information for an ecosystem is a promising avenue for determining surveillance and action-assessment points or decision thresholds. This case study presents actual values of plant species richness and evenness

and their NRV that managers of GPG vegetation can use as starting points for establishing thresholds for heightened attention or taking action in their own locations. In addition, it illustrates the limitations of using just NRV information to establish these thresholds. Continued attention to the importance of plant diversity in GPG and other ecosystems, long-term monitoring of plant diversity metrics being established by the NPS and other agencies and organizations, research to better understand the response of these metrics to various stressors and management actions, and concerted efforts by managers to determine the costs and benefits of acting at various levels of diversity will help refine decision thresholds for this vast but highly threatened ecosystem.

Acknowledgments At the time of the research for this manuscript Jayne Jonas was with IAP World Service, Inc. This project would not have been possible without access to the datasets provided by the Cedar Creek, Konza Prairie, and Shortgrass Steppe LTER Programs, the Kansas Agricultural Experiment Station—College Pasture at Hays, Kansas, and the Fort Keogh Livestock and Range Research Lab, Miles City, Montana. In particular, we thank Troy Mielke (Cedar Creek), Gene Towne (Konza), Seth Munson (SGS), and Peter Adler (Hays and Miles City) for assistance with information on the datasets. We also thank Greg Eckert, Diane Larson, and Glenn Guntenspergen for their helpful comments on an earlier version of this manuscript. Funding for this project was provided by the U.S. Geological Survey’s Park Monitoring Project. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

References

- Adler, P. B., and J. M. Levine. 2007. Contrasting relationships between precipitation and species richness in space and time. *Oikos* 116:221–232.
- Adler, P. B., W. R. Tyburczy, and W. K. Lauenroth. 2007. Long-term mapped quadrats from Kansas prairie: Demographic information for herbaceous plants. *Ecology* 88:2673.
- Albertson, F. W., and J. E. Weaver. 1944. Nature and recovery of grassland from the Great Drought of 1933 to 1940. *Ecological Monographs* 14:393–479.
- Anderson, R. C. 2006. Evolution and origin of the Central Grassland of North America: Climate, fire, and mammalian grazers. *Journal of the Torrey Botanical Society* 133:626–657.
- Anderson, J., L. Vermiere, and P. B. Adler. 2011. Fourteen years of mapped, permanent quadrats in a northern mixed prairie, USA. *Ecology* 92:1703.
- Axelrod, D. I. 1985. Rise of the grassland biome, central North America. *Botanical Review* 51: 163–201.
- Bagchi, S., D. D. Briske, X. B. Wu, M. P. McClaran, B. T. Bestelmeyer, and M. E. Fernandez-Gimenez. 2012. Empirical assessment of state-and-transition models with a long-term vegetation record from the Sonoran Desert. *Ecological Applications* 22:400–411.
- Baker, W. L. 1992. Effects of settlement and fire suppression on landscape structure. *Ecology* 73:1879–1887.
- Balvanera, P., A. B. Pfisterer, N. Buchmann, J. S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters* 9:1146–1156.
- Bennetts, R. E., J. E. Gross, K. Cahill, C. McIntyre, B. B. Bingham, A. Hubbard, L. Cameron, and S. L. Carter. 2007. Linking monitoring to management and planning: Assessment points as a generalized approach. *The George Wright Forum* 24:59–77.

- Bergeron, Y., S. Gauthier, M. Flannigan, and V. Kafka. 2004. Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. *Ecology* 85:1916–1932.
- Bestelmeyer, B. T., J. R. Brown, K. M. Havstad, R. Alexander, G. Chavez, and J. E. Herrick. 2003. Development and use of state-and-transition models for rangelands. *Journal of Range Management* 56:114–126.
- Bestelmeyer, B. T., A. J. Tugel, G. L. Peacock, Jr., D. G. Robinett, P. L. Shaver, J. R. Brown, J. E. Herrick, H. Sanchez, and K. M. Havstad. 2009. State-and-transition models for heterogeneous landscapes: A strategy for development and application. *Rangeland Ecology & Management* 62:1–15.
- Biondini, M. E., A. A. Steuter, and C. E. Grygiel. 1989. Seasonal fire effects on the diversity patterns, spatial distribution and community structure of forbs in the northern Mixed Prairie, USA. *Vegetatio* 85:21–32.
- Borchert, J. R. 1950. The climate of the central North American grassland. *Annals of the Association of American Geographers* 40:1–39.
- Briggs, J. M., A. A. K. Knapp, J. M. Blair, J. L. Heisler, G. A. Hoch, M. S. Lett, and J. K. McCarron. 2005. An ecosystem in transition: Causes and consequences of the conversion of mesic grassland to shrubland. *Bioscience* 55:243–254.
- Briske, D. D., S. D. Fuhlendorf, and F. E. Smeins. 2006. A unified framework for assessment and application of ecological thresholds. *Rangeland Ecology and Management* 59:225–236.
- Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. Downing, M. Sankaran, and C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443:989–992.
- Cardinale, B. J., J. P. Wright, M. W. Cadotte, I. T. Carroll, A. Hector, D. S. Srivastava, M. Loreau, and J. J. Weis. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences U S A* 104:18123–18128.
- Carlson, M., and W. A. Kurz. 2007. Approximating natural landscape pattern using aggregated harvest. *Canadian Journal of Forest Research* 37:1846–1853.
- Clark, C. M., and D. Tilman. 2008. Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature* 451:712–715.
- Collins, S. L. 2000. Disturbance frequency and community stability in native tallgrass prairie. *The American Naturalist* 155:311–325.
- Collins, S. L., S. M. Glenn, and D. J. Gibson. 1995. Experimental analysis of intermediate disturbance and initial floristic composition: Decoupling cause and effect. *Ecology* 76:486–492.
- Coppedge, B. R., D. M. Engle, C. S. Toepfer, and J. H. Shaw. 1998. Effects of seasonal fire, bison grazing and climatic variation on tallgrass prairie vegetation. *Plant Ecology* 139:235–246.
- Cyr, D., S. Gauthier, Y. Bergeron, and C. Carcaillet. 2009. Forest management is driving the eastern North American boreal forest outside its natural range of variability. *Frontiers in Ecology and the Environment* 7:519–524.
- DeBacker, M. D., A. N. Sasseen, C. Becker, G. A. Rowell, L. P. Thomas, J. R. Boetsch, and G. D. Willson. 2004. *Vegetation community monitoring protocol for the Heartland I & M Network and Prairie Cluster Prototype Monitoring Program*. Republic: National Park Service.
- Doyon, F., S. Yamasaki, and R. Duchesneau. 2008. The use of the natural range of variability for identifying biodiversity values at risk when implementing a forest management strategy. *Forestry Chronicle* 84:316–329.
- Duncan, S. L., B. C. McComb, and K. N. Johnson. 2010. Integrating ecological and social ranges of variability in conservation of biodiversity: Past, present, and future. *Ecology and Society* 15(1):5.
- Egan, D., and E. A. Howell, editors. 2001a. *The historical ecology handbook: A restorationist's guide to reference ecosystems*. Washington, DC: Island Press.
- Egan, D., and E. A. Howell. 2001b. Introduction. In *The historical ecology handbook: A restorationist's guide to reference ecosystems*, ed. D. Egan, and E. A. Howell, 1–23. Washington, DC: Island Press.

- Ellison, A. M. 2001. Exploratory data analysis and graphic display. In *Design and analysis of ecological experiments*, ed. S. M. Scheiner, and J. Gurevitch, 37–62. New York: Oxford University Press.
- Fargione, J., D. Tilman, R. Dybzinski, J. H. R. Lambers, C. Clark, W. S. Harpole, J. M. H. Knops, P. B. Reich, and M. Loreau. 2007. From selection to complementarity: Shifts in the causes of biodiversity–productivity relationships in a long-term biodiversity experiment. *Proceedings of the Royal Society B-Biological Sciences* 274:871–876.
- Ford, E. S., A. E. Kelly, S. M. Teutsch, S. B. Thacker, and P. L. Garbe. 1999. Radon and lung cancer: A cost-effectiveness analysis. *American Journal of Public Health* 89:351–357.
- Gibson, D. J., and L. C. Hulbert. 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. *Vegetatio* 72:175–185.
- Graves, H. S. 1899. The Black Hills Forest Reserve. In *The nineteenth annual report of the survey, 1897-1898. Part V. Forest Reserves*, 67–164. Washington, DC: U.S. Geological Survey.
- Groffman, P. M., J. S. Baron, T. Blett, A. J. Gold, I. Goodman, L. H. Gunderson, B. M. Levinson, M. A. Palmer, H. W. Paerl, G. D. Peterson, N. L. Poff, D. W. Rejeski, J. F. Reynolds, M. G. Turner, K. C. Weathers, and J. Wiens. 2006. Ecological thresholds: The key to successful environmental management or an important concept with no practical application? *Ecosystems* 9:1–13.
- Hartnett, D. C., K. R. Hickman, and L. E. Fischer Walter. 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. *Journal of Range Management* 49:412–420.
- Hartnett, D. C., A. A. Steuter, and K. R. Hickman. 1997. Comparative ecology of native and introduced ungulates. *Ecological Studies* 125:72–101.
- Harwell, M. A. 1997. Ecosystem management of south Florida. *Bioscience* 47:499–512.
- Hastings, A., and D. B. Wysham. 2010. Regime shifts in ecological systems can occur with no warning. *Ecology Letters* 13:464–472.
- Hector, A., and R. Bagchi. 2007. Biodiversity and ecosystem multifunctionality. *Nature* 448:188–191.
- Heisler, J. L., J. M. Briggs, and A. K. Knapp. 2003. Long-term patterns of shrub expansion in a C4-dominated grassland: Fire frequency and the dynamics of shrub cover and abundance. *American Journal of Botany* 90:423–428.
- Higgins, K. F. 1986. *Interpretation and compendium of historical fire accounts in the northern Great Plains. Resource Publication, 161*. Washington, DC: U. S. Fish and Wildlife Service.
- Hooper, D. U., F. S. Chapin, III, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* 75:3–35.
- Isbell, F. I., and B. J. Wilsey. 2011. Increasing native, but not exotic, biodiversity increases above ground productivity in ungrazed and intensely grazed grasslands. *Oecologia* 165:771–781.
- Knapp, A. K., J. M. Briggs, D. C. Hartnett, and S. L. Collins, eds. 1998. *Grassland dynamics: Long-term ecological research in tallgrass prairie*. New York: Oxford University Press.
- Landres, P. B., P. Morgan, and F. J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecological Applications* 9:1179–1188.
- Lauenroth, W. K., I. C. Burke, and M. P. Gutmann. 1999. The structure and function of ecosystems in the central North American grassland region. *Great Plains Research* 9:223–259.
- Magurran, A. E. 1988. *Ecological diversity and its measurement*. Princeton: Princeton University Press.
- Manier, D., D. Shorrock, E. W. Schwieger, I. W. Ashton, B. Frakes, M. Britten, D. Pillmore, and J. Burke. 2011. *Rocky Mountain Network vegetation composition structure and soils monitoring protocol: Small park grasslands, shrublands, and woodlands*, Version 1.0. Natural Resource Report NPS/ROMN/NRR-2011/383. Fort Collins, CO: National Park Service.
- Martin, J., M. C. Runge, J. D. Nichols, B. C. Lubow, and W. L. Kendall. 2009. Structured decision making as a conceptual framework to identify thresholds for conservation and management. *Ecological Applications* 19:1079–1090.

- Morgan, P., G. H. Aplet, J. B. Haufler, H. C. Humphries, M. M. Moore, and W. D. Wilson. 1994. Historic range of variability: A useful tool for evaluating ecosystem change. *Journal of Sustainable Forestry* 2:87–111.
- Mori, A. S., and K. P. Lertzman. 2011. Historic variability in fire-generated landscape heterogeneity of subalpine forests in the Canadian Rockies. *Journal of Vegetation Science* 22:45–58.
- Munson, S. M., and W. K. Lauenroth. 2009. Plant population and community responses to removal of dominant species in the shortgrass steppe. *Journal of Vegetation Science* 20:224–232.
- National Park Service. 2009. *Interim technical guidance on defining meaningful desired conditions for natural resources*. Fort Collins: National Park Service Biological Resource Management Division.
- Plumb, G. E., and J. L. Dodd. 1993. Foraging ecology of bison and cattle on a mixed prairie: Implications for natural area management. *Ecological Applications* 3:631–643.
- Ratajczak, Z., J. B. Nippert, J. C. Hartman, and T. W. Ocheltree. 2011. Positive feedbacks amplify rates of woody encroachment in mesic tallgrass prairie. *Ecosphere* 2:121.
- Risser, P. G., E. C. Birney, H. D. Blocker, S. W. May, W. J. Parton, and J. A. Wiens. 1981. *The true prairie ecosystem*. Stroudsburg: Hutchinson Ross Publishing Company.
- Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. *Ecology* 69:40–45.
- Samson, F. B., and F. L. Knopf. 1994. Prairie conservation in North America. *Bioscience* 44: 418–421.
- Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: Linking theory to observation. *Trends in Ecology & Evolution* 18:648–656.
- Schmid, B., P. Balvanera, B. J. Cardinale, J. Godbold, A. B. Pfisterer, D. Raffaelli, M. Solan, and D. S. Srivastava. 2009. Consequences of species loss for ecosystem functioning: meta-analyses of data from biodiversity experiments. In *Biodiversity, ecosystem functioning, and human wellbeing*, ed. S. Naeem, D. E. Bunker, A. Hector, M. Loreau, and C. Perrings, 14–29. Oxford: Oxford University Press.
- Sherriff, R. L., E. E. Berg, and A. E. Miller. 2011. Climate variability and spruce beetle (*Dendroctonus rufipennis*) outbreaks in south-central and southwest Alaska. *Ecology* 92:1459–1470.
- Sierra, C. A., M. E. Harmon, F. H. Moreno, S. A. Orrego, and I. J. Del Valle. 2007. Spatial and temporal variability of net ecosystem production in a tropical forest: Testing the hypothesis of a significant carbon sink. *Global Change Biology* 13:838–853.
- Smart, A. J., B. H. Dunn, P. S. Johnson, L. Xu, and R. N. Gates. 2007. Using weather data to explain herbage yield on three Great Plains plant communities. *Rangeland Ecology & Management* 60:146–153.
- Stafford Smith, M. 1996. Management of rangelands: Paradigms at their limits. In *The ecology and management of grazing systems*, ed. J. Hodgson and A. W. Illius, 325–357. Wallingford: CAB International.
- Stoddard, J. L., D. P. Larsen, C. P. Hawkins, R. K. Johnson, and R. H. Norris. 2006. Setting expectations for the ecological condition of streams: The concept of reference condition. *Ecological Applications* 16:1267–1276.
- Swanson, F. J., J. A. Jones, D. O. Wallin, and J. H. Cissel. 1994. Natural variability—implications for ecosystem management. In *Volume II: Ecosystem management: principles and applications. Gen. Tech. Rep. PNW-GTR-318*. ed. M. E. Jensen and P. S. Bourgeron, 80–94. Portland: U.S. Department of Agriculture, Forest Service.
- Symstad, A. J. 2005. A pilot study for assessing the potential plant community impacts of re-introducing grazing to Scotts Bluff National Monument: Results and implications for further investigation. Keystone: USGS Northern Prairie Wildlife Research Center, Black Hills Station.
- Symstad, A. J. 2011. A vegetation management plan for Fort Union Trading Post National Historic Site: Final report for interagency agreement number F154910005, Natural Resource Report NPS/FOUS/NRR–2011/456. Fort Collins: National Park Service.

- Symstad, A. J., and J. L. Jonas. 2011. Incorporating biodiversity into rangeland health: Plant species richness and diversity in Great Plains grasslands. *Rangeland Ecology & Management* 64:555–572.
- Symstad, A. J., R. A. Gitzen, C. L. Wienk, M. R. Bynum, D. J. Swanson, A. D. Thorstenson, and K. J. Paintner. 2011. Plant community composition and structure monitoring protocol for the Northern Great Plains I & M Network: Version 1.00, Natural Resource Report NPS/NRPC/NRR–2011/291. Fort Collins: National Park Service.
- Teeri, J. A., and L. G. Stowe. 1976. Climatic patterns and the distribution of C⁴ grasses in North America. *Oecologia* 23:1–12.
- Thompson, J. R., S. L. Duncan, and K. N. Johnson. 2009. Is there potential for the historical range of variability to guide conservation given the social range of variability? *Ecology and Society* 14(1):18.
- Thrush, S. F., J. E. Hewitt, P. K. Dayton, G. Coco, A. M. Lohrer, A. Norkko, J. Norkko, and M. Chiantore. 2009. Forecasting the limits of resilience: Integrating empirical research with theory. *Proceedings of the Royal Society B-Biological Sciences* 276:3209–3217.
- Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs* 57:189–214.
- Tilman, D. 2001. Effects of diversity and composition on grassland stability and productivity. In *Ecology: Achievement and Challenge*, ed. M. C. Press, N. J. Huntly, and S. Levin, 183–207. Cambridge: Cambridge University Press.
- Tilman, D., and A. El Haddi. 1992. Drought and biodiversity in grasslands. *Oecologia* 89:257–264.
- Towne, E. G., D. C. Hartnett, and R. C. Cochran. 2005. Vegetation trends in tallgrass prairie from bison and cattle grazing. *Ecological Applications* 15:1550–1559.
- Unnasch, R. S., D. P. Braun, P. J. Comer, and G. E. Eckert. 2009. The ecological integrity assessment framework: A framework for assessing the ecological integrity of biological and ecological resources of the National Park System. Fort Collins: National Park Service.
- Webb, W. L., S. R. Szarek, W. K. Lauenroth, R. S. Kinerson, and M. Smith. 1978. Primary productivity and water use on native forest, grassland, and desert ecosystems. *Ecology* 59: 1239–1247.
- Webb, W. L., W. K. Lauenroth, S. R. Szarek, and R. S. Kinerson. 1983. Primary production and abiotic controls in forests, grasslands, and desert ecosystems in the United States. *Ecology* 64:134–151.
- Wienk, C., A. Thorstenson, J. Freeman, and D. Swanson. 2009. Northern Great Plains Fire Ecology Program Review 1997–2007. Internal report, U.S. Department of Interior, National Park Service, Midwest Regional Office, Fire & Aviation Management, Omaha, Nebraska.
- Wohl, E. 2011. What should these rivers look like? Historical range of variability and human impacts in the Colorado Front Range, USA. *Earth Surface Processes and Landforms* 36:1378–1390.
- Zavaleta, E. S., J. R. Pasari, K. B. Hulvey, and G. D. Tilman. 2010. Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proceedings of the National Academy of Sciences U S A* 107:1443–1446.