RANK CLOCKS AND PLANT COMMUNITY DYNAMICS

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Abstract. Summarizing complex temporal dynamics in communities is difficult to achieve in a way that yields an intuitive picture of change. Rank clocks and rank abundance statistics provide a graphical and analytical framework for displaying and quantifying community dynamics. We used rank clocks, in which the rank order abundance for each species is plotted over time in temporal clockwise direction, to display temporal changes in species abundances and richness. We used mean rank shift and proportional species persistence to quantify changes in community structure in long-term data sets from fertilized and control plots in a late successional old field, frequently and infrequently burned tallgrass prairie, and Chihuahuan desert grassland and shrubland communities. Rank clocks showed that relatively constant species richness masks considerable temporal dynamics in relative species abundances. In the old field, fertilized plots initially experienced high mean rank shifts that stabilized rapidly below that of unfertilized plots. Rank shifts were higher in infrequently burned vs. annually burned tallgrass prairie and in desert grassland compared to shrubland vegetation. Proportional persistence showed that arid grasslands were more dynamic than mesic grasslands. We conclude that rank clocks and rank abundance statistics provide important insights into community dynamics that are often hidden by traditional univariate approaches.

Key words: community dynamics; proportional persistence; rank-abundance curves; rank clock; rank shifts; species diversity; temporal dynamics.

INTRODUCTION

Many analyses of long-term data demonstrate that ecological communities are spatially and temporally dynamic. Indeed, many of our most fundamental ecological models and concepts, such as island biogeography (MacArthur and Wilson 1967), metacommunity dynamics (Leibold et al. 2004), succession (Clements 1916), neutral models (Hubbell 2001), and community stability (Ives and Carpenter 2007) are based on temporally dynamic phenomena, yet they are frequently tested with spatial rather than temporal data. Moreover, long-term data sets may capture dynamics, but existing statistical tools may fail to fully quantify, summarize,

and interpret predictions from dynamic models. As the portfolio of long-term data sets continues to grow in number, length, and complexity, new analytical and visualization tools will be needed to understand pattern and change in ecological communities. Although a variety of tools exists (e.g., McCune and Grace 2002, Magurran 2004), detailed long-term data sequences present new challenges along with the potential for new insights into how and why communities are changing (Magurran 2007). Thus, additional tools are needed to better test dynamic model predictions and understand temporal dynamics of communities.

Environmental drivers may lead to internal community "reordering" along environmental gradients prior to compositional change (M. D. Smith, A. K. Knapp, and S. L. Collins, *unpublished manuscript*). Thus, robust mechanisms to quantify within-community reordering or stability are needed. Consistent rank-abundance

curves, species–area curves, or diversity are often used as signs of system stability or self-organization (Leibold et al. 1997, Shurin 2007). However, stability measured at such aggregate levels can mask temporal shifts in the internal dynamics of a community, such as species turnover or changes in relative abundance among species. Species turnover or similarity/dissimilarity metrics offer one approach to quantifying aggregate internal dynamics (Collins 2000, Vellend 2001, Goheen et al. 2005), yet these metrics may be highly sensitive to variation in rare species, and are presented in arbitrary units, hindering comparison among sites.

To address these needs, we explore two techniques to describe internal community temporal dynamics. The first, rank-abundance curves, is not new (e.g., Bazzaz 1975), but has generally not been used in the context of temporal dynamics of mature communities. The second, rank clock and associated metrics, is borrowed from studies of urban demography (Batty 2006) and has utility both as a visualization and quantification tool.

Caused in part by interest in the neutral theory of community structure and biodiversity (Hubbell 2001), rank-abundance curves and curve-fitting procedures have experienced a resurgence (McGill et al. 2006). Rank-abundance curves, such as the log-normal or broken-stick models, have a long history in ecological research (Preston 1948, Whittaker 1965, Wilson 1991), yet their utility continues to be debated (McGill 2003, McGill et al. 2007). Common criticisms are that (1) more than one mechanism can produce the same pattern, (2) they use free parameters of questionable ecological relevance to maximize fit, (3) determining which model generates the best fit is challenging, and (4) they may result from non-ecological phenomena such as the central limit theorem (McGill 2003, but see Allen et al. 2001, Alonso et al. 2008). Despite these criticisms, rank-abundance curves remain a widely used tool even if such curves lack strong mechanistic inference and are simply descriptive. As such, they yield little more information than normative diversity indices in assessing community dynamics, and they lack metrics needed to describe internal dynamics in meaningful ways.

The rank clock, as used in urban demography applications (Batty 2006), visually represents temporal changes in richness and rank abundance in community data sets, exposing rich dynamical behavior that is lost with traditional curve-fitting procedures. This visualization is superior to simple presentations of rank-abundance curves because rank clocks encompass both aggregate and internal dynamics. In addition, two associated indices, proportional persistence and mean rank shift, can be used to quantify aspects of internal community dynamics in time series data. This combination of visualization and rank shift metrics can describe internal community dynamics over time in ways that standard techniques do not.

To illustrate these techniques, we used long-term plant community data sets from three LTER sites, contrasting temporal change in fertilized and control plots at Cedar Creek, annually burned and infrequently burned prairie at Konza Prairie, and desert grassland and shrubland vegetation at Sevilleta. We used rank clocks and rank abundance statistics to visualize and quantify internal community dynamics. We demonstrate how rank clocks and rank–abundance statistics provide important insights into community dynamics that are often hidden by the more commonly used univariate or curve-fitting approaches.

Methods

Study sites

Because we are using previously published data, only a brief description of each data set is provided here. Cedar Creek Natural History Area is located in the prairie–forest border region of southern Minnesota, USA. We used data from a late successional old field (Field C) abandoned from agriculture in 1934. Beginning in 1982, six replicates of 4 × 4 m control and annually fertilized (9.52 g N/m^2 of NH_4NO_3) plots were sampled annually for species composition by clipping a 0.3 m^2 area, sorting to species, drying and weighing the samples. Common species in control plots include *Schizachyrium scoparium*, *Artemisia ludoviciana*, *Poa pratensis*, *Sorghastrum nutans*, and *Solidago nemoralis*. For more details, see Tilman (1987).

Konza Prairie Biological Station is a 36-km² topographically diverse area of native tallgrass prairie in northeastern Kansas, USA, which is divided along watershed boundaries into 64 management units ranging in size from 12 to 136 ha. Replicate management units are burned at 1-, 4-, and 20-yr intervals. We used data from 20 permanently marked 10-m² circular quadrats located in similar upland areas that were either burned annually or infrequently (once every 20 years). Cover of each species in each quadrat was visually estimated each year using a modified Daubenmire percent cover scale. Cover of each species was determined by converting the Daubenmire scale to the midpoint of the cover range. Species maximum annual cover values were used in all analyses. Common species include *Andropogon gerardii*, *Schizachyrium scoparium*, *Sorghastrum nutans*, *Ambrosia psilostachya*, *Artemisia ludoviciana*, *Aster ericoides*, *Solidago missouriensis*, and *S. canadensis*. For more details, see Collins and Smith (2006).

The Sevilleta LTER site is located in the Sevilleta National Wildlife Refuge (SNWR), a 100 000-ha area along the Rio Grande in central New Mexico, USA. The SNWR occurs at the transition between Great Plains grassland and Chihuahuan Desert grassland and shrubland biomes. We used data from permanent plots in black grama (*Bouteloua eriopoda*) grassland and creosotebush (*Larrea tridentata*) shrubland. In each plant

community, vegetation was measured for 10 years in 36 permanently located 1-m^2 quadrats arrayed in an evenly spaced (5.8 m) 6×6 grid within each of four 36×36 m blocks. The cover of all plant species in each quadrat was visually estimated each year. In addition to black grama and creosotebush, common species include *Sporobolus* spp., *Sphaeralcea wrightii*, *S. leptophylla*, *Lesquerella fendleri*, *Chamaesyce* spp., and *Muhlenbergia torreyi*. For more details, see Báez et al. (2006).

Data analyses

Curve-fitting.—Wilson (1991) provided a summary of community structure models and procedures for fitting some of the commonly used rank-abundance curves. The models, which include geometric series, log-normal, veiled log-normal, Zipf, and Zipf-Mandelbrot, have been operationalized in the vegan routine in R. We used vegan to determine which models best fit each year of data in our three long-term data sets. The best fit model was determined for each experiment in each year based on the deviance criterion determined as the minimization of sum of squares of deviations from predicted and observed values (Wilson 1991).

Rank clocks.—Following Batty (2006) we used rank clocks, in which the rank order abundance for each species is plotted starting with a vertical axis at 12 o'clock (assuming a 12-year data set). The most important species (assigned rank 1) is plotted at the bottom of the vertical axis, with decreasing rank at progressively higher positions along the axis. Year 2 rank data are then plotted in the same order along a second axis that would represent one o'clock, year 3 at two o'clock, and so on. Species rank changes can then be plotted in temporal clockwise direction by connecting the ranks on each axis from one year to the next to display changes in species abundances and richness over time. If no changes occurred in composition and relative rank this would result in a clock with a series of concentric, non-overlapping circles (see Appendix). The distance from the origin along an axis represents the number of species measured for a particular year, so rank clocks simultaneously display changes in rank abundance and species richness. In real data sets, species composition and abundances change based on environmental fluctuations or experimental treatments creating more complex patterns in time. We illustrate rank clocks with data from fertilized and control plots at Cedar Creek.

Temporal dynamics.—We used two measures of community change. Mean rank shift (MRS) quantifies relative changes in species rank abundances, an indicator of shifts in relative abundance over time. MRS is calculated as

$$\text{MRS} = \sum_{i=1}^{n}(|R_{i,t+1} - R_{i,t}|)/n \tag{1}$$

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. Proportional persistence (PP) quantifies relative species gains and losses from one year to the next, scaled to the year of interest, and is calculated as

$$\text{PP} = (s_t \cap s_{t+1})/S_{t+1} \tag{2}$$

where $s_t \cap s_{t+1}$ is the number of species in common in years t and $t + 1$ standardized to S, the total number of species in year $t + 1$. We illustrate the utility of proportional persistence and mean rank shift with data from all three sites.

A program to create rank clock plots and calculate the indices mean rank shift and proportional persistence is available online at the Sevilleta LTER web site.[12]

RESULTS

Curve-fitting failed to differentiate changes in community structure that occurred between within-site comparisons at two of the three sites (Table 1). Based on the deviance criterion, the log-normal distribution provided the best fit in 45 of 100 possible cases. The mathematically related veiled log-normal had the best fit in another 28 cases, and the Zipf-Mandelbrot provided the best fit in 21 cases. The niche preemption model provided a very poor fit to all data sets. Of greater significance is that the log-normal generally provided the best fit to the grass and shrub communities at Sevilleta and fertilized and control plots at Cedar Creek despite the dramatic differences in species composition (shrubs vs. grasses at Sevilleta) and richness (25 vs. 15 species, on average, at Cedar Creek) within communities at each site. Clear differences occurred among model fits for the annually burned and infrequently burned sites at Konza. The Zipf-Mandelbrot model was the best fit in 14 of 18 cases in the annually burned grassland, whereas the log-normal, veiled log-normal, and Zipf functions were nearly equally robust in infrequently burned grassland. However, there was no clear temporal pattern to which model fit best in the infrequently burned site. Together these results suggest that best fit models vary unpredictably within a site over time, and have limited power to discriminate between communities with dramatically different composition and diversity.

The temporal variability and internal dynamics of rank-abundance curves from Cedar Creek show how changes in relative ranks lead to changes in shape among rank-abundance curves that are difficult to quantify in a way that intuitively relates to temporal dynamics (Fig. 1). We highlight the relative importance of two key species in this system, the late successional native perennial C_4 grass, *Schizachyrium scoparium*, and the early successional exotic annual C_3 grass, *Agropyron repens*. In control plots, *Schizchyrium* was nearly always the highest-ranked species subject to minor fluctuations, whereas *Agropyron* was lower ranked, somewhat vari-

TABLE 1.   Curve-fitting results for three long-term data sets.

Model	Cedar Creek		Konza Prairie		Sevilleta	
	Control (yr)	Fertilized (yr)	Unburned (yr)	Burned (yr)	Grassland (yr)	Shrubland (yr)
Preemption	0	0	0	0	0	0
Log-normal	15	18	7	2	1	2
Veiled log-normal	0	3	6	2	9	8
Zipf	0	1	5	0	0	0
Zipf-Mandelbrot	7	0	0	14	0	0

Notes: Values are the number of years within a site that fit each model. Treatments include control and fertilized plots in Field C at Cedar Creek, Minnesota, from 1982 to 2003; infrequently and frequently burned grassland at Konza Prairie, Kansas, from 1984 to 2001; and desert grassland and shrubland communities at the Sevilleta National Wildlife Refuge, New Mexico, from 1995 to 2004. Curve-fitting was done with the vegan routine in R. A detailed description of the models can be found in Wilson (1991).

able, but persistent. In fertilized plots, there was a dramatic shift in ranks that occurred within five years following the start of fertilizer application in which *Agropyron* became dominant and eventually *Schizachyrium* became nearly undetectable. None of this type of change would be captured in aggregate community indices, such as species richness or rank-abundance curves.

Rank clocks are able to visualize the complex changes and dynamics that can occur over time even in communities not subjected to experimental manipulation (Fig. 2a). Essentially, ranks tend to fluctuate in control plots and diversity changes from one year to the next in response to interannual variability. In comparison, the rapid loss in diversity can be seen in the fertilized treatments despite considerable fluctuations in relative ranks (Fig. 2b). By plotting a subset of the data, rank clocks can effectively display the dramatic changes in rank abundance shown in Fig. 1. In the control rank clock, *Schizachyrium* and *Agropyron* fluctuate from year to year but generally retain their relative rank positions (Fig. 2c), whereas, in the fertilized rank clock (Fig. 2d), *Schizachyrium* spirals out of its dominant ranking while *Agropyron* spirals inward.

The MRS analysis quantifies the dynamics exhibited in the rank clocks. MRS was relatively stable over time in control plots at Cedar Creek but decreased rapidly after the start of the fertilizer treatment, only to level off at a rate lower than that of the controls and with lower interannual variability (Fig. 3a). That is, based on MRS, once the new dominance pattern emerged, fertilized plots were generally more stable than control plots. At Konza Prairie, MRS in annually burned and unburned plots was comparable for eight years until 1992 when MRS increased in both burning treatments then decreased in annually burned prairie and remained consistently lower than in infrequently burned grassland (Fig. 3c). Desert grassland had consistently higher MRS values than creosotebush shrubland at the Sevilleta; thus, rank abundances were less stable in grassland than in shrub-dominated areas (Fig. 3e). Thus, the MRS analysis quantified internal dynamical processes not revealed by rank-abundance curves.

Mean species PP decreased rapidly over the first five years of fertilizer application at Cedar Creek before returning to comparable but highly variable levels similar to control plots (Fig. 3b). Mean species PP was highly variable at Konza Prairie but was generally higher in annually burned compared to infrequently burned areas (Fig. 3d). At Sevilleta, mean species PP was similar in grassland and shrubland communities (Fig. 3f). However, mean species PP in desert grassland was generally lower than in the two mesic grasslands. This reflected greater system response to interannual variation in precipitation in desert grasslands than in mesic prairies. Thus, mean species PP measured internal compositional consistencies not detectable using only rank-abundance curves.

DISCUSSION

Most well understood measures of community structure (e.g., diversity indices, rank-abundance curves, species–area curves) have advantages in some contexts and limitations in others. Many such measures represent a "snapshot in time" yet many ecological models are dynamic and require insight into patterns and mechanisms that change over time. As long-term data sets increase in breadth, length, and scope, better visualization tools and analytical methods will be needed to quantify temporal dynamics in ecological communities (MacNally 2007, Alonso et al. 2008). We propose the use of (1) rank clocks to visualize complex temporal dynamics, and (2) measures of internal dynamics, such as mean proportional persistence and mean rank shift, that quantify change in community structure over time. These indices are not meant to replace existing well-known measures of community structure. Rather, they add new dimensions to our understanding of what aspects of communities are changing over time.

Curve-fitting provided little insight into internal community dynamics at Sevilleta and Cedar Creek despite substantial differences in drivers of community dynamics at each site (C$_3$ shrubland vs. C$_4$ grassland at Sevilleta, control vs. fertilized plots at Cedar Creek). Curve-fitting procedures have been subjected to considerable attention, analysis, and criticism (Whittaker 1965,
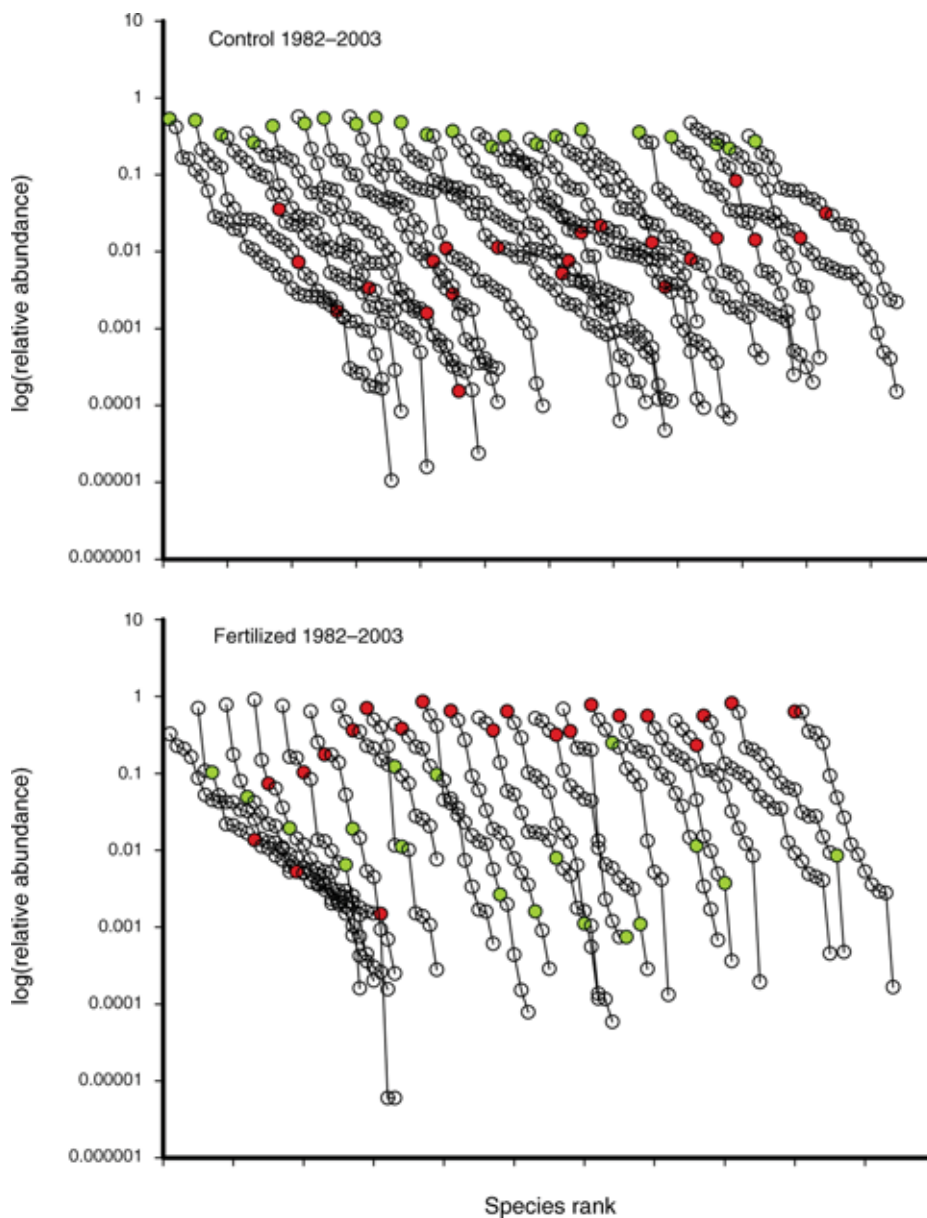
FIG. 1.   Annual rank-abundance curves for control and fertilized plots at Cedar Creek Field C from 1982 to 2003 showing the relative ranking of *Schizachyrium scoparium* (solid green circles), a late-successional, perennial C_4 grass, and *Agropyron repens* (solid red circles), an early-successional, annual C_3 grass. The curves show how the ranks of *Schizachyrium* and *Agropyron* remain relatively constant in control plots but rapidly reverse order in fertilized plots.

Wilson 1991, McGill 2003, McGill et al. 2007). A common concern is that the mathematical constructs behind some models have little biological meaning. This is particularly true with the log-normal distribution and its variants, which can, under certain restrictions (Alonso et al. 2008), be derived as a product of the central limit theorem (McGill 2003). Indeed, 73 of our 100 analyses (Table 1) were best described by the log-normal or veiled log-normal distributions. Nekola and

Brown (2007) found that a wide variety of data sets, many of which were unrelated to biological systems, were also described by the log-normal distribution suggesting some universal commonality in rank abundance distributions. On the other hand, given the common patterns found in interactive (species) and non-interactive (Cowboy Junkies play lists) data sets, this result could easily be attributed to statistical artifact of little biological or mechanistic significance (Nekola
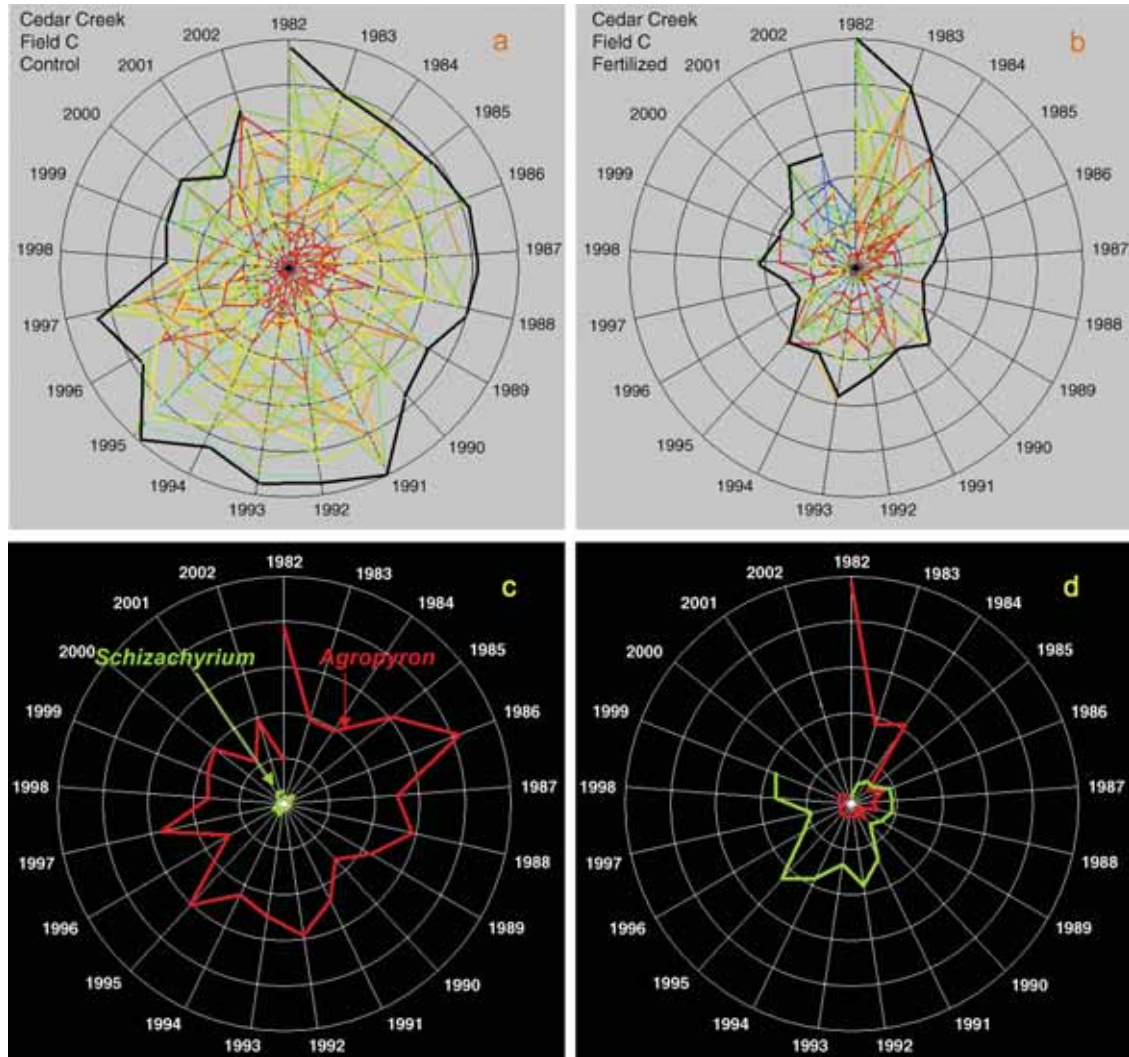
FIG. 2.   Rank clock plots for Cedar Creek (a) control and (b) fertilized plots showing complex temporal dynamics in rank shifts and total species richness over time. Species are plotted in order of rank importance starting in the center and moving outward along each axis. Rank clock plots for individual species show how ranks of two contrasting species, *Schizachyrium scoparium* (green line) and *Agropyron repens* (red line) either (c) remain relatively constant in control plots or (d) spiral in or out of importance in fertilized plots. See Appendix for details on rank clocks.

and Brown 2007). Until such issues are resolved, curve-fitting will remain at best a weak test of ecological theory (McGill 2003, McGill et al. 2007).

A second common problem is that curve-fitting procedures retain no information about species identity and are thus not suited to detecting shifts in the identity of dominant or rare species. Such internal community dynamics are often the response of interest in manipulative experiments or long-term data sets (Fig. 1). Rank clocks provide an objective procedure to display internal changes in community structure over time. These clocks display not only species richness but also the variability in rank abundance patterns among species in a community. The rank clocks from Cedar Creek clearly

show the decrease in species richness in response to fertilization relative to the control (Tilman 1987), a common response in many herbaceous plant communities (Suding et al. 2005). Although the data could be plotted along a linear time-axis, temporal sequences of rank-abundance curves are rarely if ever used. Plotting temporal data as a rank clock generates a more compact graphic device, yields a different visual dynamic than a linear plot (see Appendix), gives a clear perception of temporal change, allows visual comparison of dynamics over time, and provides rapid visual assessment of differences between starting and ending configurations. Thus, we believe that rank clocks provide a useful tool for visualizing complex community dynamics.
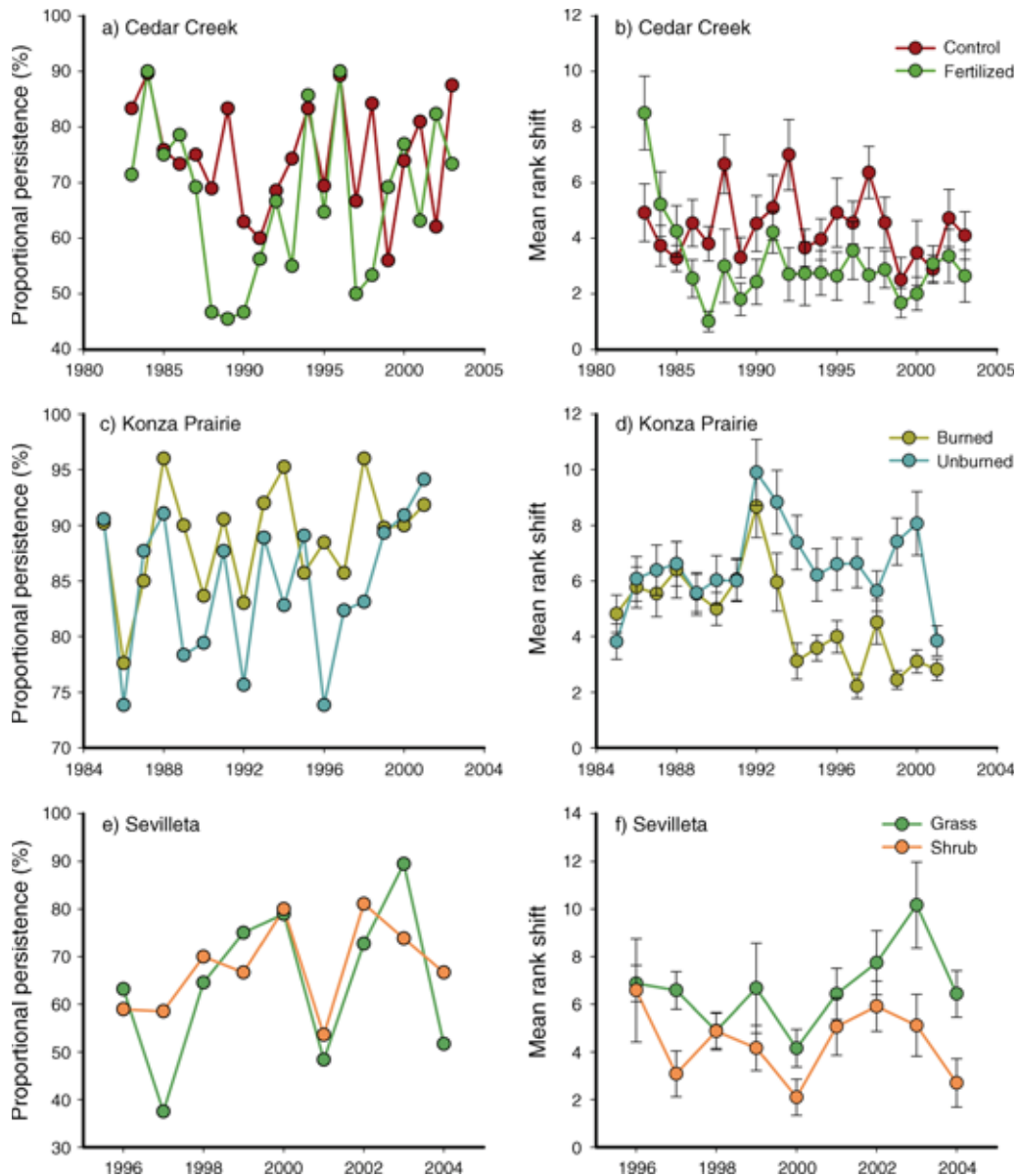
FIG. 3.   Mean rank shift and percentage proportional persistence (i.e., proportional persistence × 100) for plant communities in (a, b) control and fertilized plots in a Minnesota old field, (c, d) annually and infrequently burned tallgrass prairie in Kansas, and (e, f) desert grassland and shrubland in New Mexico, USA.

Quantitative assessments of community stability in response to environmental drivers are important goals for ecological research (Peters et al. 2004, Ives and Carpenter 2007). Proportional persistence and mean rank shifts are two quantitative measures of community stability. Both measures provided unique information on the rapid changes in composition and rank abundance in the N fertilization experiment at Cedar Creek (Tilman 1987), as well as community response to burning at Konza Prairie, and differential community dynamics in grass- and shrub-dominated vegetation at

Sevilleta. Specifically, mean rank shift clearly documented the rapid transition and stabilization of communities following N addition at Cedar Creek, dynamics not detected with curve-fitting or changes in species richness. Nevertheless, these results highlight the fact that apparently stable distributions of species rank–abundances mask complex temporal dynamics (Batty 2006). This suggests the need for a more process-oriented approach to analyzing long-term ecological experiments, with many tools yet to be developed, as patterns may not be as predictive as previously anticipated.

With increasing interest in understanding community dynamics, particularly in response to rapid environmental change, we will need to employ more tools in addition to traditional univariate and curve-fitting procedures. While these measures are clearly important, other important aspects of community dynamics will be missed without attention to the pattern of change in species abundances and internal community dynamics, yet these aspects are much less frequently examined. Thus, we argue for use of a different suite of quantitative measures of both internal and aggregate community structure to better understand temporal dynamics of ecological communities.

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APPENDIX

Figures showing construction of a rank clock in which the rank order abundance for each species in a community sample is plotted at each time interval in temporal clockwise direction, rank clock display of a 20-yr data set with 25 species in which no species turnover (gains or losses) or changes in rank abundance occur over time, and a conceptual diagram illustrating two-species dynamics in linear and rank clock format (*Ecological Archives* E089-201-A1).