RELATIONSHIPS AMONG INDICES SUGGEST THAT RICHNESS IS AN INCOMPLETE SURROGATE FOR GRASSLAND BIODIVERSITY

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Abstract. Although many indices estimate diversity, species richness recently has been used as a surrogate for diversity in many studies in ecology, biogeography, and conservation. Underlying assumptions of this approach are that all diversity indices, including those that weight species importance by their relative abundance (e.g., evenness), are correlated positively, and that richness accounts for a large proportion of the variance in diversity. We addressed these assumptions with data from six grassland sites using univariate and multivariate analyses of a variety of indices (species evenness, richness, rarity, dominance, and Simpson's diversity index). Univariate correlations between plant species evenness and richness were weak and negative at each site. Principal-component analyses consistently revealed two significant components of variation in diversity. Richness and evenness were largely orthogonal, with Simpson's diversity loading between them. Thus, measures of species diversity based on relative abundance, as well as richness, may be necessary to capture the full complexity of diversity in conservation studies and in experiments of biodiversity and ecosystem functioning. At these and perhaps other sites, species richness was an incomplete surrogate for diversity.

Key words: biodiversity; diversity indices; dominance; grasslands; rarity; species evenness; species richness.

INTRODUCTION

Biodiversity represents the complexity of life on Earth, and has phenotypic, genotypic, taxonomic, and ecological dimensions that can be measured within taxa (e.g., genetic diversity), across taxa (e.g., species diversity), or across ecosystems (e.g., landscape diversity; Wilson and Peter 1988, Solbrig et al. 1994, Gaston and Spicer 1998). Important conceptual components of species diversity include richness, evenness, dominance, and rarity of species. These components are characterized by the way in which the presence of each species is weighted by an aspect of importance such as abundance or biomass (Hill 1973, Magguran 1988). With species richness, each species contributes to diversity in the same manner regardless of its abundance or biomass. Some measures, such as species evenness, weight each species by its relative abundance or biomass. Species diversity indices (e.g., Simpson's $1/D$ or Shannon's H′) represent composite measures, and are sometimes designed so that richness and evenness are mathematically independent (Smith and Wilson 1996). Other measures focus on a restricted subset of species.

Species dominance (e.g., Berger-Parker index) is the relative importance of the one species contributing the most to total abundance or biomass. In contrast, species rarity is a measure of the proportion of species that meet the restriction that their relative abundance or biomass is below some threshold (e.g., average relative abundance or biomass, or $<1/S$, Camargo 1992).

Even though the taxonomic dimension of biodiversity comprises a number of components, each operationally defined by a number of indices, species richness has been used recently as a surrogate for diversity in general (Schluter and Ricklefs 1993, Rosenzweig 1995, Gaston 1998, Tilman and Lehman 2002), especially in biogeography and conservation (Brown 1995, Andelman and Willig 2003, Willig et al. 2003). Species richness is relatively easy to measure compared to other indices because relative abundance does not have to be measured. However, implicit assumptions of this surrogate approach are that (1) richness and evenness are correlated positively and strongly, and (2) species richness accounts for a large proportion of the variance in diversity. According to this viewpoint, diversity is essentially a one-dimensional concept that can be estimated with species richness alone.

The few empirical studies that have tested these assumptions suggest that diversity components, specifically richness and evenness, may not be correlated positively. Buzas and Hayek (1996) decomposed Shannon's diversity index into richness and evenness com-

ponents and found that they can each affect H' of forest communities in different and sometimes counteracting ways. Stirling and Wilsey (2001) combined published data from a variety of sources and found that correlations between species richness and evenness (J') were strongly positive for invertebrate animals and weakly positive for vertebrates, but negative for plants. Stevens and Willig (2002) showed that spatial variation in richness was independent of variation in evenness in New World bat communities, with diversity emerging as a balance of richness and evenness.

We analyze empirical data from several North American grasslands, and examine univariate and multivariate relationships among a variety of measures of plant species diversity. Such relationships have been studied with simulated data (e.g., Pielou 1966, Hurlbert 1971, DeBenedictus 1973, Hill 1973, Peet 1974, Kempton 1979), but rarely with empirical data (but see Stirling and Wilsey 2001, Stevens and Willig 2002). Our approach differs from that of Stirling and Wilsey (2001) in three ways. First, we analyzed relationships at the focal scale of a quadrat within each of a number of grassland sites, whereas Stirling and Wilsey (2001) combined data across sites and studies for plant analyses. Second, we used the Simpson's diversity index ($1/D$) because its associated measures of evenness and richness are mathematically independent (Smith and Wilson 1996) and it has desirable statistical properties (May 1981, Lande 1996). Consequently, the identification of a significant relationship between Simpson's evenness and species richness would suggest that biological processes constrain their values to covary; otherwise the values should be mathematically independent of each other. Finally, and perhaps most importantly, we used principal-components (PC) analysis to determine if variation in multiple measures of diversity collapse into a single dimension (one important PC) in which all measures vary in a similar fashion or whether covariation among measures is sufficiently complex to require two or more dimensions (two or more PCs) to understand variation among plots. Our objectives were to (1) quantify relationships among different components of diversity, and (2) determine if richness accounts for most of the variation in diversity within sites.

METHODS

We analyzed data (Table 1) from three Long-term Ecological Research (LTER) sites (Inouye et al. 1987, Milchunas et al. 1990, Huberty et al. 1998) and three sites in Texas (Wilsey and Polley 2003, Polley et al. 2005). These sites were: Cedar Creek (CDR), Kellogg Biological Station (KBS), Short-grass Steppe (SGS), Temple Grassland (TG), Temple Prairie remnant (TP), and Parkhill Prairie (PHP). Investigators at each site clipped plots, and then sorted aboveground biomass by species in each quadrat. These data were then used to calculate relative biomass and a number of species di-

versity indices. Plots containing woody species were excluded from analysis.

The CDR and KBS sites are old fields dominated by a variety of early successional C_3 grass species (CDR) and perennial forbs (KBS), whereas the SGS site is short-grass prairie dominated by the C_4 grass *Bouteloua gracilis*, and includes plots from several sites with moderate to no grazing by cattle. Consideration of grazing intensity effects was beyond the scope of this synoptic study. The KBS site was established on plowed and abandoned ground in 1989, and underwent typical succession from annual dicots and monocots to perennial dicots during the time period encompassed by the data set. The TG site consisted of four fields with different times since grazing by cattle that were dominated by the C_4 grass *Bothriochloa ischaemum* (Wilsey and Polley 2003), and included plots with litter removed or left remaining. Litter removal had no effect on any diversity measure or biomass (Wilsey and Polley 2003), and did not appreciably change relationships among diversity indices when litter-removal plots were analyzed separately. TP is a 3-ha never-plowed tallgrass prairie remnant dominated by *Schizachyrium scoparium*, *Sorghastrum nutans*, and *Andropogon gerardii* that was last burned two years before sampling (Wilsey and Polley 2003). PHP is a 21-ha never-plowed remnant dominated by *Sorghastrum nutans*, *Tripsacum dactyloides*, *Schizachyrium scoparium*, and a variety of forbs (Polley et al. 2005). PHP was managed by The Nature Conservancy for many years before sampling, and was last burned a year and a half before sampling. All three Texas sites occur within the blackland prairie region and are classified as sub-humid grasslands (TP, PHP) or successional sub-humid grasslands (TG).

To capture different aspects of species diversity, we considered five different indices: Simpson's diversity ($D = 1/\Sigma p_i^2$), where p_i is the proportional biomass of species i; species richness (S); species evenness (D/S); Berger-Parker dominance (maximum proportional biomass, Berger and Parker 1970); and rarity. Species richness is the number of species that occurred in a sampling unit. Rarity was defined as the proportion of species whose relative biomass was $<1/S$ (Camargo 1992).

Empirical relationships among components of diversity were quantified with correlation and principal-components analyses (PCA). Principal components were based on correlation matrices, and were interpreted and presented if eigenvalues were ≥ 1 (Kaiser 1960). The importance value (IV) of a particular index in differentiating among sampling units in the PCA was calculated as $IV_i = \Sigma r_{ij}^2 \times R_j^2$ where i represents a particular diversity index, j represents a particular principal component (PC), r_{ij} is the correlation coefficient between diversity index i and PC_j, and R_j^2 is the proportion of variation among sampling units represented by PC j (Lacher and Willig 1995, Willig and Hollander 1995). Principal-components analyses were conducted individually for each of the six sites (Table 1), but were

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TABLE 1.   Information on the six U.S. grassland study sites.

Site (State)	Code	Description	Years		Quadrats	
			Actual	No.	No.	Size (m²)
Cedar Creek (Minnesota)	CDR	old field	1988–1996	9	56	0.3†
Kellogg Biological Station (Michigan)	KBS	old field	1989–2001	13	30	1
Short-grass Steppe (Colorado)	SGS	short-grass steppe	1992–1998	7	105	0.25
Parkhill prairie (Texas)	PHP	blackland prairie	2001	1	12	0.5
Temple grassland (Texas)	TG	old field	2001	1	40	0.5
Temple Prairie (Texas)	TP	blackland prairie	2001	1	10	0.5

† At Cedar Creek, an area 0.1×3 m was clipped; all others were square in shape.

not done across sites because the size of the sampling units differed among sites and many aspects of diversity are scale dependent (Scheiner et al. 2000, Willig et al. 2003). Annual mean values for each quadrat were used at sites with multiple years because PCA gave consistent results when each year was analyzed separately. All analyses were conducted with SAS (SAS Institute 2000).

RESULTS

Correlations between indices

The correlation between species evenness and richness was negative at each site, although in the two smaller data sets the association was not significant (Table 2). A Fisher's test (Sokal and Rohlf 1995) for combining independent probabilities was highly significant ($G = 68.7$, df $= 12$, $P < 0.001$), suggesting that the nonsignificant correlations were the result of insufficient power and that the preponderance of data support a significant negative relationship. The strongest correlation between Simpson's diversity and a particular component was with dominance (ranging from -0.90 to -0.96, Table 2). Evenness and richness were each correlated positively with Simpson's diversity. Evenness was correlated negatively with rarity at each site (Table 2).

PCA

Within each site, multivariate analysis consistently revealed two components of variation in diversity. The loadings on the two principal components were similar at all sites (Fig. 1). All of the indices except species richness loaded strongly on PC1, with species richness loading on both PC1 and PC2 (Fig. 1). PC1 accounted for 53–74% of the variation (eigenvalues and R^2, respectively, for: CDR: 2.7, 53.1; SGS: 2.7, 54.8; KBS: 2.8, 55.6; PHP: 3.4, 67.3; TG: 2.7, 53.3; TP: 3.7, 73.6) and PC2 accounted for 23–38% of the variation (CDR: 1.9, 38.2; SGS: 1.8, 36.5; KBS: 1.8, 36.6; PHP: 1.1, 22.9; TG: 1.9, 37.9; TP: 1.2, 24.3) within sites. Importance values, which quantify the relative importance of each index in explaining overall variation, were fairly similar among indices, but generally were higher for Simpson's diversity and dominance in the Texas sites (Fig. 1). At all sites, a consideration of loadings on PC1 and PC2 showed that Simpson's diversity was in-

termediate between richness and evenness (Fig. 1), and that evenness and richness were largely orthogonal.

DISCUSSION

During 1960–1980, diversity usually was estimated with compound indices that incorporated both richness and evenness, or each of these components was calculated and interpreted separately (Magguran 1988). However, in more recent years, species richness has been the sole index of species diversity in almost all studies of biodiversity and ecosystem functioning (Kinzig et al. 2002, Loreau et al. 2002) and in studies within the fields of conservation biology (Andleman and Willig 2003, Willig 2003) and biogeography (Brown 1995, Rosenzweig 1995, Willig et al. 2003). It also is used as the only component of diversity in some tests of the intermediate-disturbance hypothesis (Huston 1994, Mackey and Currie 2001). The implicit assumptions of this approach, that all diversity indices are strongly correlated (e.g., DeBenidictis 1973) and that richness accounts for the largest proportion of variance in diversity, were not supported by our analyses.

Overall, we found that variation in species richness and evenness were largely orthogonal, and that Simpson's diversity loaded intermediately between them. We say ''largely orthogonal'' because species richness and evenness were correlated weakly and negatively at each site, that is, angles between loading vectors were slightly greater than 90° (Fig. 1; see also Table 1). Despite these weak correlations, evenness and other measures based on relative abundance provided a significant amount of information on variation in species diversity that was independent of that provided by species richness alone (Fig. 1).

Although we looked at five conceptually distinct components of diversity, all of which are commonly measured in the literature, we found that only two principal-components (PC) dimensions were necessary to characterize variation within sites. The fact that we consistently found differences in PC loadings among measures suggests that there are clear differences in what each measure represents. This supports the view that plant diversity cannot be encapsulated by species richness alone, as is implicitly assumed when the terms ''diversity'' and ''richness'' are used interchangeably (e.g., Rickleffs and Schluter 1993:4, Rosenzweig 1995:

TABLE 2. Pairwise correlation coefficients between measures of species diversity within six grassland sites in North America.

Site	Rarity	Evenness	Richness	Diversity
Kellogg Biological Station, (Michigan, USA)				
Dominance	0.44***	−0.38***	−0.58***	−0.90***
Rarity		−0.81***	−0.17	−0.44***
Evenness			−0.36***	0.36***
Richness				0.67***
Short-grass Steppe (Colorado, USA)				
Dominance	0.36***	−0.54***	−0.52***	−0.93***
Rarity		−0.71***	0.31***	−0.28***
Evenness			−0.35***	0.48***
Richness				0.62***
Cedar Creek (Minnesota, USA)				
Dominance	0.44***	−0.45***	−0.46***	−0.91***
Rarity		−0.76***	0.33***	−0.34***
Evenness			−0.44***	0.36***
Richness				0.58***
Parkhill Prairie (Texas, USA)				
Dominance	0.59*	−0.91**	−0.11	−0.96***
Rarity		−0.70*	0.11	−0.62*
Evenness			−0.22	0.90**
Richness				0.23
Temple grassland (Texas, USA)				
Dominance	0.40*	−0.49**	−0.49**	−0.95***
Rarity		−0.70***	0.34*	−0.30
Evenness			−0.46**	0.41**
Richness				0.55***
Temple Prairie (Texas, USA)				
Dominance	0.85**	−0.82**	−0.47	−0.96***
Rarity		−0.95***	−0.08	−0.82**
Evenness			−0.09	0.75*
Richness				0.57

Notes: Dominance is the relative biomass of the species with greatest biomass (Berger and Parker 1970); rarity is the proportion of species with biomass $<1/S$ (Camargo 1972); evenness is Simpson's evenness ($1/D/S$); richness is the number of species per plot; and diversity is Simpson's diversity ($1/D$). Significance is denoted by * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

201, Tilman and Lehman 2002:14). However, the number of dimensions in describing variation in diversity may depend on underlying environmental gradients to which each measure of diversity responds, as well as the scale of measurement. Factors that may enhance the likelihood that different sites would exhibit similar patterns of variation include similar species pools, common underlying environmental gradients, and comparable spatial scales with respect to focus and extent. If environmental gradients that cause variation within sites differ among sites, or if environmental gradients affecting differences in diversity among sites are distinct from those responsible for variation in diversity within sites, we might expect dissimilar patterns. Within this context, the consistent results at our six sites is not surprising—we focused on short-stature vascular plant communities from grassland biomes in the United States that have been sampled at similar spatial scales. If scale differences were greater among sites, or if we focused on different community types at different sites, or if we evaluated patterns that transpired across biome boundaries, we might have required fewer or more dimensions to capture salient features of variation. Future

research should investigate how environmental gradients affect the strength and form of the association among diversity components.

Studying how richness and evenness interact will enhance our understanding of biodiversity as a whole (e.g., Buzas and Hayek 1996, Stirling and Wilsey 2001, Stevens and Willig 2002, Willig et al. 2003). For example, numerous studies have found that evenness and richness respond differently to grazing (McNaughton 1977, King and Pimm 1983, Altesor et al. 1998, Alados et al. 2003, Wilsey and Polley 2003), fertility (e.g., Piper 1995), top predator control (e.g., Chalcraft and Resetarits 2003, Schmitz 2003), and latitude (e.g., Stevens and Willig 2002). From a conservation perspective, species richness, evenness, and diversity may not respond in the same manner to habitat fragmentation or loss, making impacts difficult to forecast without a consideration of all these elements (Gorresen and Willig 2004).

Tokeshi (1993) and Magguran and Phillip (2001) suggested that rarity (defined here as the proportion of rare species in the community) is caused mostly by a lengthening of the "tail" of rank–abundance relation-
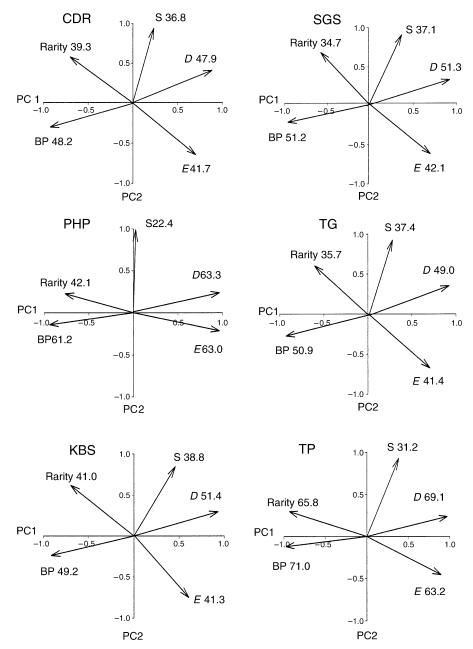
FIG. 1. Principal-components analysis (PCA) loadings of diversity indices from Cedar Creek (CDR), short-grass steppe (SGS), and Kellogg Biological Station (KBS) LTER sites, and three blackland prairie sites within Texas (Parkhill Prairie [PHP], Temple grasslands [TG], and Temple Prairie [TP]). Importance values are presented at the end of each arrow for species richness (S), Simpson's diversity (D), evenness (E), Berger-Parker dominance (BP), and proportion of rare species (Rarity).

ships (i.e., by an increase in species richness) due to migration of rare species. A prediction stemming from this hypothesis is that empirical relationships between richness and rarity should be strongly positive. We found that rarity was weakly and inconsistently correlated with species richness. However, correlations between rarity and evenness were consistently and strongly negative (Table 2). This suggests that rarity might

be influencing diversity more through the evenness dimension than through the richness dimension.

A key reason (e.g., Rosenzweig 1995, Gaston 1998) for using only species richness to characterize diversity is its relative ease of measurement. Accurately measuring the relative abundance of all species is more difficult. However, if a simple, easy-to-measure surrogate of species diversity is required in appropriately

sized samples, we suggest that the Berger-Parker dominance measure might provide a superior alternative to richness. To estimate it, it is only necessary to know the abundance (or biomass) of the most abundant species, and total abundance (or biomass). In fact, the identities of species other than the most abundant species need not be determined. It may provide a useful surrogate for diversity because it (1) is easily measured in samples, (2) accounts for as much or more variation in diversity, and (3) should be less dependent on sample size than species richness. Indeed, the inverse form of the index may be preferable as a diversity index, because it increases as diversity increases (Magurran 1988).

We found that importance values were roughly similar for the five diversity indices, which suggests that all of them can be useful in describing variation in diversity. Species richness was as good as any other in the three sites with large sample sizes, but it did not stand out as being more important than other indices. Thus, these empirical results suggest that to more completely characterize variation within grassland sites, or to estimate diversity in a more comprehensive manner, measures based on relative abundance, in addition to richness, are much better than richness alone (Collins 1990, Buzas and Hayek 1996, Chapin et al. 2000, Purvis and Hector 2000, Stirling and Wilsey 2001). Indeed, species evenness and dominance can have important effects on net primary productivity, invasion resistance, and local extinction (Nijs and Roy 2000, Wilsey and Potvin 2000, Foster et al. 2002, Wilsey and Polley 2002, Smith and Knapp 2003, Smith et al. 2004, Wilsey and Polley 2004) that are independent of species richness. D. R. Chalcraft, B. J. Wilsey, C. M. Bowles, and M. R. Willig (*unpublished manuscript*) examined relationships between biomass and multiple measures of diversity at the same sites considered here and found that the shape (linear vs. quadratic) and direction (positive vs. negative) of the relationship were different for different measures of diversity. For example, at one site (Cedar Creek, Minnesota, USA), the relationship was positively linear between richness and biomass but relationships were quadratic between Simpson's diversity and biomass and negatively linear between evenness and biomass. This suggests that the form of the relationships can change depending on which measure is being used. Based on this and the fact that much of the variation in diversity remains unaccounted for when using only richness, we suggest that conservation and biodiversity studies should move beyond using species richness as the sole index of diversity, thereby attaining a more complete understanding of diversity.

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