DINTERIA No. 31: 50-66 – Windhoek, Namibia – 2009/2010

Diversity measures in comparative rangeland studies: application and advantages of Species Abundance Distributions and diversity profiles

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Abstract
Biodiversity consists of the two components richness and evenness. Diversity indices such as the Shannon or Simpson index are commonly used to describe diversity patterns for sampled habitats or plant communities. However, these indices are ineffective for comparing richness and evenness at the same time. This might lead to a biased interpretation of actual diversity patterns. With this article we aim at describing two alternative approaches for comparing diversity patterns that, in combination, allow an effective visualisation of those patterns; curves for ranked species abundance distributions and diversity profiles. In a case study scenario, we compare biodiversity measurements within and between a Thornbush savannah and the Nama Karoo. Furthermore, we briefly discuss possible applications of these methods in rangeland and restoration ecology.

Keywords: conservation; biodiversity; species richness; evenness; species abundance distribution; diversity ordering; savannah

Introduction

Originating from the rather scientific and value neutral term biological diversity, the more ethical and valuable expression 'biodiversity' was coined by Edward O. Wilson at a conference for conservation biologists and was spread later on with a book called "biodiversity" (Wilson & Osbourne, 1988). Today, an overwhelming amount of studies was undertaken on the subject of biodiversity in various disciplines, not only in biology itself, but also in physics, mathematics, philosophy and economy. To this day, the protocol "Convention on Biological Diversity", formulated in Rio de Janeiro 1992, was ratified by 168 countries worldwide (www.cbd.int). This treaty mandates national environmental organizations worldwide to ensure a sustainable use of biodiversity and assure its conservation.

The scientific term 'biodiversity' or 'biological diversity' in general is descriptive for the variation of life at different levels of organization, such as the diversity of genes, species,

populations and ecosystems. By this, a versatile perception of the irreplaceable importance of biodiversity evolved in terms of (i) the ecological services it can provide (Myers, 1996; Hooper et al., 2005), (ii) the economical values it contains (Pimentel et al., 1997; Weikard, 2002), and (iii) also its philosophical and ethical values (Takacs, 1996; Oksanen & Pietarinen, 2004). From a more statistical point of view there are various ways of how to measure biodiversity. Much has been published on the measurement of biodiversity (Williams & Gaston, 1994; Rousseau & Van Hecke, 1999; Magurran, 2004; Stohlgren, 2007), but still uncertainty remains regarding the comparison of biodiversity measurements (Gotelli & Colwell, 2001; Maurer & McGill, 2004; Kindt *et al.*, 2006).

A common approach to compare samples containing information on biodiversity is to calculate diversity indices, e.g. Shannon or Simpson's Index, and to determine whether there are significant differences or not. The variety of techniques and indices developed for the analysis of biodiversity does not make it easier to choose the right tool for comparing biodiversity measurements (Magurran, 2004). The most frequently used index today is simply the number of species in a sample, termed species richness (or species density if it was sampled for a defined area). In fact, biodiversity consists of two components, richness and evenness. The latter one is related to the abundance of the species in the sample. Species abundance data are counts of individuals but equally, percent plant cover or the biomass of a species can be used (Magurran, 2004). However, besides the hard to interpret Shannon Index of diversity (Magurran, 2004), which allows incorporating both richness and evenness, all diversity indices are just univariate measures of one component of diversity. Thus, species richness alone cannot tell us the whole story about the diversity of a community. This was also suggested by Wilsey *et al.* (2005), who compared univariate measures of plant diversity of temperate grasslands for their importance using a multivariate approach. The author found that species richness does not stand out as a single all explaining surrogate for biodiversity. Thus, analyses based only on species richness without considering evenness might miss important information in describing biodiversity.

The problem of incomplete measures of biodiversity has been recognized in ecological literature, and more visual and complex methods for comparison were developed. In this study we address two of these approaches for the comparison of (i) different plant communities and/or habitats, as well as (ii) measures of biodiversity by using datasets from semi-arid savannah rangelands in Namibia. In order to contrast different communities or habitats, curves of ranked species abundances, so called species abundance distributions (SAD), were applied. These depict a characteristic distribution for a sampled habitat according to the richness and the evenness of the species found. Recently, the SADs were again proposed as useful tools, and thus a revival in ecology is in sight (Magurran, 2007; McGill *et al.*, 2007).

The second technique applied allows a sound comparison of diversity measurements, and results within and among certain plant communities or habitats. Richness and evenness measures cannot be compared effectively, yet both are important to describe diversity. To incorporate both aspects, a method that provides an ordering of samples according to both richness and evenness was needed. Patil and Taillie (1977) developed a technique called

diversity ordering, a method in which multiple diversity measures are implemented at once and communities or samples are displayed as curves. These diversity curves, called diversity profiles (Kindt & Coe, 2005), allow a visual and quantitative comparison of multiple aspects of diversity.

With this article we want to actively revive the usage of species abundance distributions and the diversity ordering technique for conservation management and ecological research. By describing the methods with a case study from southern and central Namibia we want to show the simplicity of the methods and demonstrate their effectiveness in comparing diversity patterns within and between ecosystems. However, it is worth to mention that the intention of this article is rather to give an overview of the methods, than interpreting patterns found in an ecological context. Suggestions for possible applications in conservation management and environmental science will be addressed briefly in the discussion section.

Study area

The four study sites are situated in southern and central Namibia (Figure 1) along a precipitation gradient oriented from north to south. Climate is semi-arid with an average annual rainfall of about 250 - 350 mm.

The rainy season is summer (October - April), but rainfall pattern shows a high interannual and spatial variability.

The two most southern study sites Niko-North (NIK-N) and Niko-South (NIK-S) are located in a communal area approximately 90 km south of Mariental (NIK-N: 25°20’01”, 17°50’58”; NIK-S: 25°20’34”, 17°50’22”). The rangeland is fenced allowing resting periods for the vegetation at NIK-N and NIK-S, respectively.

Figure 1: *Location of test sites along the trasect of BIOTA Southern Africa, indicated by white arrows.*

The adjacent sites are grazed rotationally mainly by goats. Vegetation is best described as an open grassy shrubland with trees growing only scattered, and is typical for the Nama Karoo biome (Palmer & Hoffman, 1997). The two northern study sites, Otjamongombe (OTJ) and Omatako-Ranch (OMA), are commercial livestock and game farms, respectively, located about 130 km south of Otjiwarongo (OMA: 21°28'53", 16°43'39"; OTJ: 21°35'48", 16°56'06"). Following Giess (1971), both sites fall into the vegetation zone of the Thornbush savannah. Vegetation is characterized by a continuous grass and herb layer and more or less dense stands of mainly thorny shrubs and small trees (mostly *Acacia* spp.). On each of these four farms a test site of one square kilometre was established by the BIOTA Southern Africa biodiversity monitoring project (www.biota-africa.org).

Methods

Field data

All four test sites are 1 km x 1 km in size. Each square kilometre was subdivided into 100 plots of 1 ha and stratified according to occurring habitat types. Within these strata 20 hectares were selected by a random sampling procedure considering the relative dominance of each type of habitat. On each of these 20 selected hectares of each test site, one central monitoring plot of 1000 m² (20 m x 50 m) was established. On these plots, plant species composition and cover was monitored within the rainy season on a yearly basis since 2001. The monitoring data used for this paper are from April 2005 for OMA and OTJ and from April 2007 for NIK-N and NIK-S, respectively.

SAD Curves

SAD Curves, which are also called Rank – Abundance Dominance (RAD) or Dominance / Diversity plots (Whittaker, 1965), display logarithmic species abundances against species rank order. The calculation of these curves is in fact relatively simple. Firstly, the species in the community are ranked according to their total abundance for all records within the respective habitat or study site. Secondly, the ranked species are plotted on the X-axis and their log abundance on the Y-axis. Resulting curves usually show a declining trend, revealing several important aspects to interpret the diversity of the samples considered. Plotting several SADs in one graph allows for visual comparison of the diversity patterns of several communities at once. Important features of these plots are the relative abundance of common and rare species. There is usually a tail of species depicting the number of species that occur only once in the community (Murray *et al.*, 1999), and a larger set of species with intermediate abundance and usually some more common species. Occasionally, there are a few very dominant species that might be considered as indicators, e.g. for mass occurrences of invasive plants, blooms of therophytes or bush encroached habitats. It is possible to fit a mathematical model to a SAD curve, such as a log-normal or broken stick distribution, in order to test against a specific null-hypothesis. Up to now, it is still debated which model best describes the process that leads to a certain community structure (McGill *et al.*, 2007), e.g. competition for niche space. We think, including mathematical models will rather increase the complexity of the

method than increase its applicability. Therefore, it will suit our purpose to simply analyse the resulting curves by visual and numerical comparison.

SAD curves were created for each single test site, and finally plotted together for an overall comparison. Abundance values used throughout the whole study do not rely on counts of individual plants but are based on plant cover estimates, i.e. for one curve the cumulative cover value of a certain species from all 20 plots per test site was used. Cover estimates as a proxy for abundance is commonly used and widely accepted in vegetation ecology (Magurran 2004).

Diversity Profiles

The core idea for ordering diversity indices from richness to evenness is based on the work of Álfred Rényi (1961) who developed a generalized entropy formula based on the concept of Shannon's entropy (Shannon, 1948), which plays a central role in information theory. In the 1970s, Hill (1973) and Pielou (1975) recognized that three diversity indices mostly used by ecologists are specific cases of Rényi's entropy formula: species richness, Shannon Diversity and Simpson Diversity. Later, Kindt *et al.* (2006) added the Berger-Parker Index. The Simpson and the Berger Parker Index are measures of dominance (evenness), whereas the Shannon Diversity Index mixes richness and evenness. Diversity profile values (H-alpha) were calculated from the frequencies of each component species (proportional abundances p_i = abundance of species i/ total abundance) and a scale parameter (α) ranging from zero to infinity (Tóthmérész, 1995) as:

$$H_\alpha = \frac{\ln\left(\sum p_i^\alpha\right)}{1-\alpha}$$

The four diversity measures are related to respective values of the scale parameter α, H_0 = species richness, H_1 = Shannon Diversity, H_2 = Simpson Diversity and H_∞ = Berger-Parker Index (Legendre & Legendre, 1998, Kindt *et al.* 2006):

$$H_0 = \ln(S)$$

$$H_1 = H = -\sum p_i \log\ p_i$$

$$H_2 = \ln(D^{-1}) = \ln\left(\sum (p_i^2)^{-1}\right)$$

$$H_\infty = \ln(d^{-1}) = \ln(p_{max}^{-1})$$

A given community A is truly more diverse than community B if the diversity profile for community A is everywhere above the diversity profile for community B. Communities that have intersecting profiles can only be partially ordered in diversity. Intersecting profiles (partial diversity ordering) demonstrates why ordering techniques such as the Rényi series are needed, since a single diversity index will not provide sufficient information. The values of the series for the four BIOTA test sites were calculated for the scales of $\alpha = \{0, 0.25, 0.5, 1, 2, 4, 8, \infty\}$ and plotted as diversity profiles for each related pair (OMA and OTJ, NIK-N and NIK–S) and for all sites together in a single graph.

Software

All analyses were carried out using R (R Development Core Team, 2005), a statistical software freely downloadable from www.cran.r-project.org. The following packages were used

to calculate the statistics: *vegan* (Oksanen et al., 2005) and *BiodiversityR* (Kindt & Coe, 2005). Graphics were produced within R and optimized using SigmaPlot Version 10.0 (Systat Software, 2006).

Results

SAD curves

The species abundance distribution for each test site is presented in Figure 2. The distribution for NIK-N reveals a relatively short range of total species (n=23) on the x-axis. There is one dominant species, a set of more common species (n=2 – n=11), and several rare species. The tail consists of six rare species that only show up once over all 20 sampled plots. There is almost a linear decrease in ranked abundance, yet distorted by one dominant species. The ten

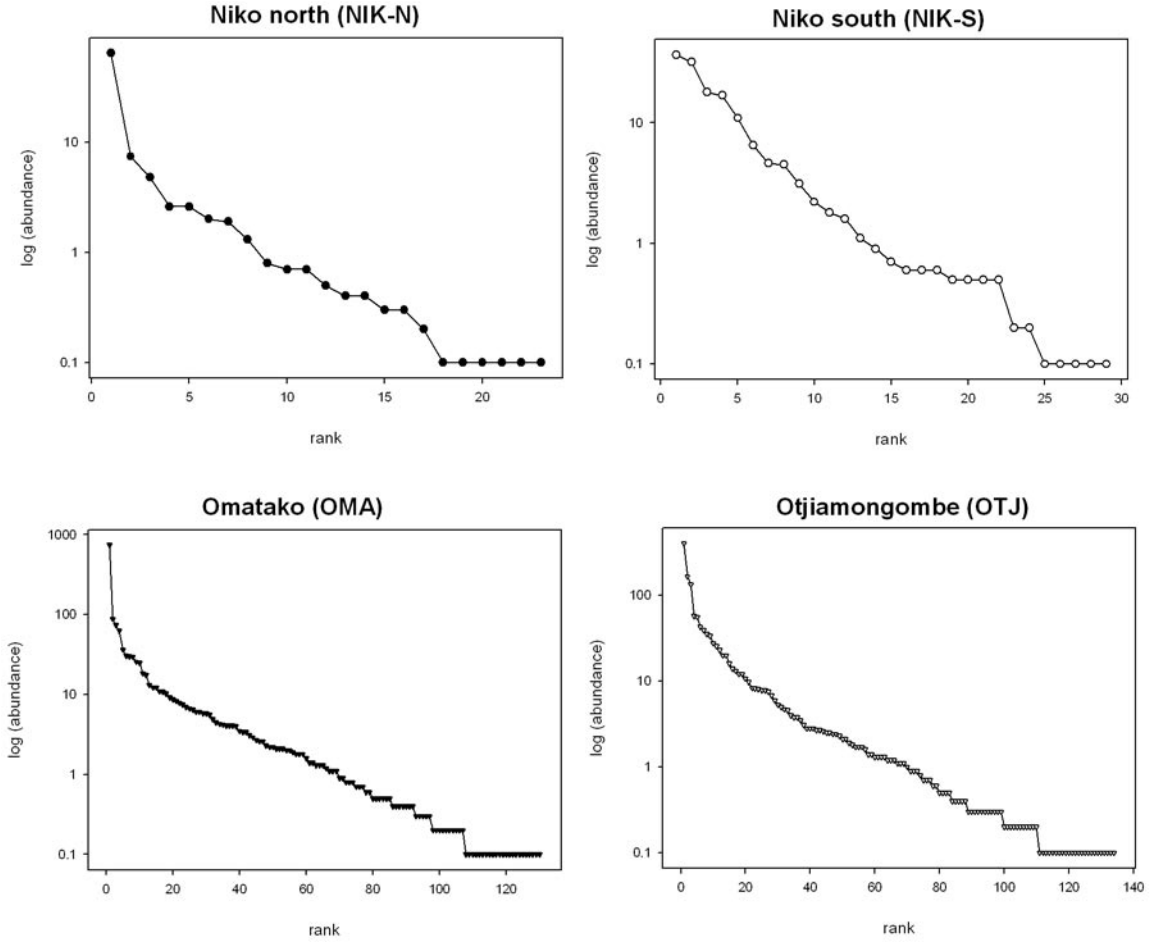

Figure 2: *Species abundance distributions for the four test sites. Upper row showing the test sites Niko north (NIK-N) and Niko south (NIK-S), the lower row Omatako (OMA) and Otjiamongombe (OTJ). Abundance is based on cumulative cover values per species per test site.*

Table 1: *Ranks of the 10 most abundant species on the four test sites according to Figure 2 and their average abundance per site (n = 20 plots). The calculated average abundance is based on cover values (%). Values for test sites NIK-S and OTJ are given in bold.*

	Rank									
NIK-N / **NIK-S**	1	2	3	4	5	6	7	8	9	10
Acacia nebrownii	**25**									
Asteraceae sp.										**2**
Boscia foetida							**3**			
Calicorema capitata			5			**5**				
Catophractes alexandri							2	**3**		
Geigeria pectidea									1	
Lycium bosciifolium										1
Phaeoptilum spinosum			**12**			2				
Rhigozum trichotomum	70			**12**						
Salsola spp.		8								
Stipagrostis anomala									**2**	
Stipagrostis hochstetteriana								2		
Stipagrostis uniplumis		**22**		3						
Xerocladia viridiramis					3					
Ziziphus mucronata					**7**					
OMA / **OTJ**	1	2	3	4	5	6	7	8	9	10
Acacia mellifera		6/**12**								
Acacia reficiens				4					**3**	
Albizia anthelmintica									2	
Aristida congesta				**4**						
Aristida rhiniochloa					**4**					
Enneapogon cenchroides								**3**		
Eragrostis annulata							2			
Eragrostis lehmanniana							**3**			
Eragrostis porosa			5							
Gisekia africana										**2**
Grewia flava						**3**				
Leucosphaera bainesii										2
Lycium eenii						2				
Monechma genistifolium			**10**							
Pogonarthria fleckii					3					
Requienia pseudosphaerosperma								2		
Stipagrostis uniplumis	51/**30**									

most abundant species for all test sites are given in Table 1. For NIK-N the most dominant species reaching a cumulative cover value of about 70% is *Rhigozum trichotomum*. NIK-S has 29 species in total, and shows a similar shape of the curve like NIK-N, except that there is no dominant species. The general pattern shows that there are more abundant species on NIK-S than on NIK-N.

The lower left graph in Figure 2 shows the SAD for OMA, which has a total number of 130 species, where we find 40 rare species, a large set of intermediate and common species, and four abundant species. The shape of the curve shows a slight linear decrease but is distorted by the more abundant species. The lower right graph in Figure 2 for OTJ shows again a similar picture, with around 134 species in total, yet a longer tail and less intermediate species. The highest abundance found on OTJ equals 403 percent summed up for all 20 hectares. The general shape of the curve is more elbow-like than a straight linear decrease.

A direct comparison of the four test sites allows distinguishing the characteristic pattern of a particular environment (Figure 3). The two long curves with the many 'tail species' and the highest abundance values are the test sites from the thornbush savannah, whereas the shorter and steeper curves come from the Nama Karoo test sites.

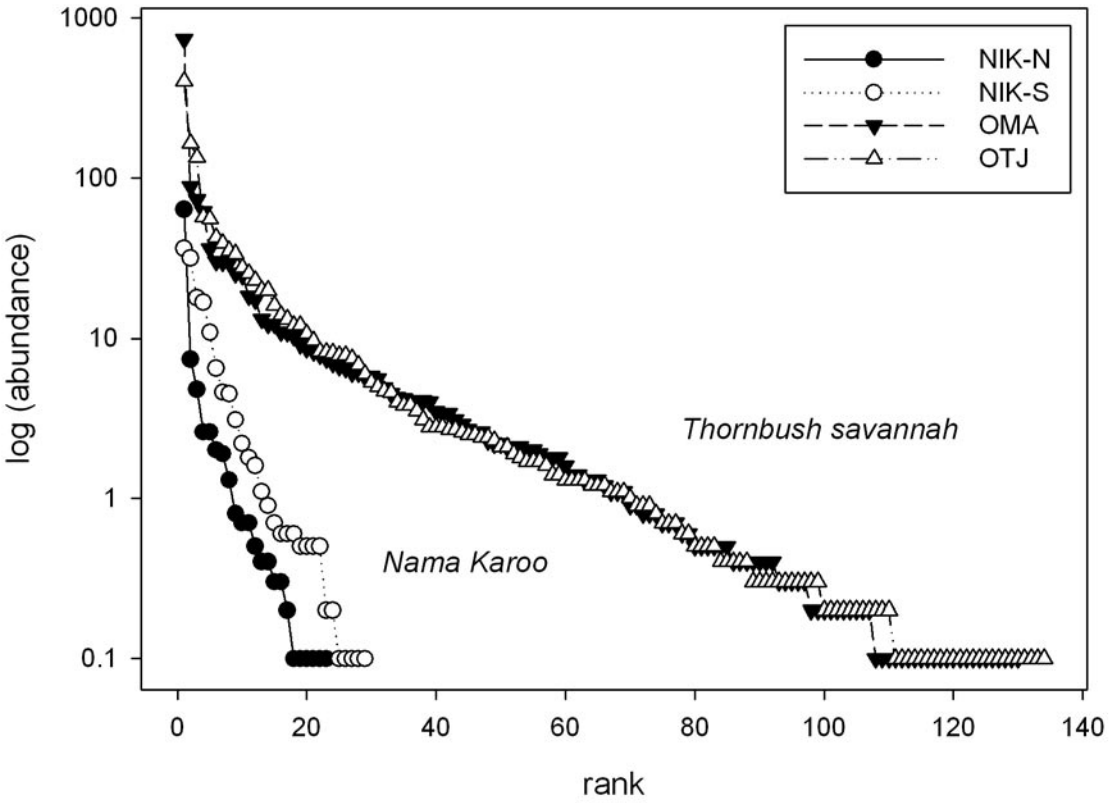

Figure 3: *Species abundance distribution for Thornbush savannah and Nama Karoo test sites*

Diversity Profiles

The diversity profiles of all four test sites are presented in Figure 4. The profile for NIK-S is consistently higher than that of NIK-N, whereas the values for species richness at H_0 are still rather tight for both test sites. The curve for NIK-N shows a clear bend towards low values of H-alpha at higher scales of alpha. The lowest values for NIK-N are at H∞ with 0.35, NIK-S yields 1.38. OTJ has consistently higher values than that of OMA. Both test sites have rather similar values for species richness at H_0, but they spread at higher scales of alpha.

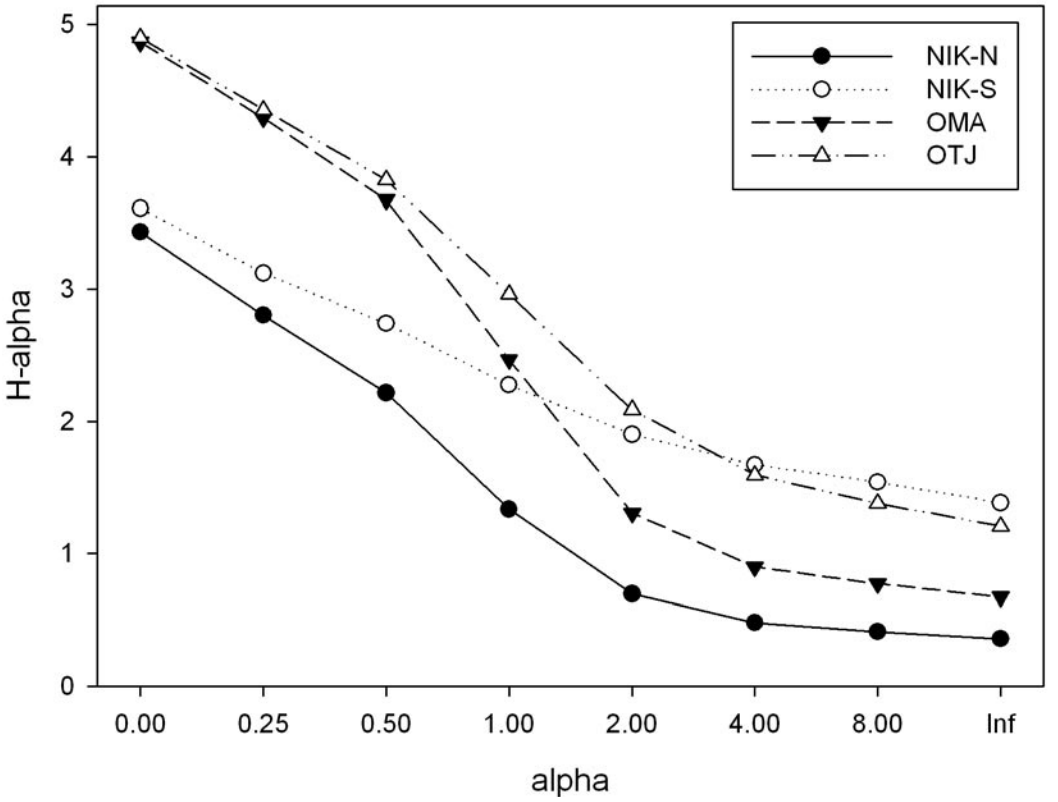

Figure 4: *Diversity profiles for Thornbush savannah sites, Omatako (OMA) and Otjiamongombe (OTJ), and Nama Karoo test sites, Niko north (NIK-N) and Niko south (NIK-S)*

The Thornbush savannah sites OMA and OTJ have much larger values at H_0 and H_1 (H_1 representing Shannon's Diversity) than the Nama Karoo test sites. Comparing the two different regions, it reveals that OTJ and NIK-N show a similar shape, although NIK-N is less diverse on all scales. In contrast, OMA begins approximating the curve of NIK-N from H_2 on, representing the Simpson Index. However, from scales larger than H_2 OTJ crosses the curve of NIK-S. NIK-S shows no steep decline. Looking at H_0 and H_4, it becomes obvious that NIK-S cannot be ranked highest according to richness, but it possesses the most even community structure of all test sites. Values for relevant scales of alpha at all sites are given in Table 2.

Table 2: *H-alpha values for important scales of α. Also listed are, species richness (S) and evenness at H_1 ($E_{1,0}$).*

Test sites	H_0	H_1	H_2	H_∞	$E_{1,0}$	S
NIK-N	3.43	1.33	0.69	0.36	0.12	23
NIK-S	3.61	2.28	1.90	1.38	0.26	29
OMA	4.87	2.47	1.31	0.67	0.09	130
OTJ	4.90	2.96	2.09	1.21	0.14	134

Discussion

Species Abundance Distributions

The grazing history of the test site Niko is inexplicit as we did not get any reliable data on the management practice applied over the last decades. NIK-N and NIK-S are situated each in one of three camps in total which are grazed in a rotational manner. This grazing regime has been retained unchanged for several years (Sarah Boeck, resident of Namibia, 2008, personal communication). However, Akhtar-Schuster, who monitored vegetation dynamics on the NIK test sites from 2001 to 2003, was given contrary information by the local community (Mariam Akhtar-Schuster 2009, personal communication). According to this, the northern camp (location of NIK-N) has been under sustained intense grazing for many years opposed to the southern camp (location of NIK-S), which was always used as a grazing reserve. Species abundance distributions for NIK-N (Figure 2, top left) and NIK-S (Figure 2, top right) clearly show different patterns that might reflect the results of different grazing regimes. On NIK-N there is a single dominant species (*Rhigozum trichotomum*), whereas no similar pattern can be found for NIK-S. For NIK-N *R. trichotomum* is ranked first with very high values of cover (≈ 70%) for the whole 20 hectares sampled. *Salsola* sp. and *Calicorema capitata* are the second and third most abundant species and reach much lower values (Table 1). Due to its clonal growth *R. trichotomum* often grows in dense stands. This shrub is reported to be an invasive species in the Kalahari region that spreads especially after heavy grazing (Thomas & Twyman, 2004). It can be hypothesized that the mass occurrence found on NIK-N is due to high grazing pressure in the past, and thus the occurrence of *R. trichotomum* in the reserve camp is less prominent. In contrast, the grass shrub ratio on NIK-S corresponds to a shrubland savannah in good condition (proportion of the grass *Stipagrostis uniplumis* ≈ 20%), whereas perennial grasses are far less abundant on NIK-N (proportion of *S. uniplumis* ≈ 3%) indicating a stronger grazing pressure on this valuable and palatable grass. However, although adjacent, not all 20 hectares on NIK-N and NIK-S are comparable concerning the

types of habitat. Therefore, further studies addressing the spatial heterogeneity and associated vegetation patterns could give more insights whether the prominence of *R. trichotomum* on NIK-N is related rather to grazing or habitat characteristics and whether more suitable habitat conditions for the growth of *S. uniplumis* occur on NIK-S, respectively. However, the pattern for NIK-S indicates a more intact and less disturbed environment. No extreme values are found and a steady decline in ranked abundances is observed ending up with a short 'step' of rare species. Furthermore, ranked abundances identify *Acacia nebrownii* and *S. uniplumis* as the two most abundant species, whereas *R. trichotomum* reached rank four. The tree *Ziziphus mucronata* occurs with a single individual only on the whole 20 hectares sampled, but appears on the fifth rank. This is because of its high cover value compared to that of shrubby and herbaceous plants, most of them which are ranked much lower. If count data would have been used instead, *Z. mucronata* would have lined up in the tail of the distribution, becoming a rare species. It is unclear how to deal with this special case, but we think that it is rather circumstantial as long as such a species is ranked in between 'common' and 'rare'.

A similar picture to NIK-N and NIK-S can be found for the Thornbush savannah sites OMA and OTJ. Here, the SAD for OMA (Figure 2, bottom left) shows an extremely high value for the first ranked species, followed by three relatively dominant species. The four highly ranked species (Table 2) are characteristic for a grass-shrub matrix occurring in savannahs (*S. uniplumis* 60%, *A. mellifera* 7 %). The graph for OTJ (Figure 2, bottom right) shows a less extreme but still similar picture. Some dominant species can also be found here, the first two are similar to OMA. In relation to species richness, both curves show similar lengths and only little variation in the overall shape. OTJ seems to have slightly more rare species than OMA; 50 species with values smaller than 0.5 % cover for 20 hectares found on OTJ, while 44 rare species were found on OMA. Dominant species might be intuitively interpreted as a result of bad management, e.g. encroaching species rise steadily in dominance (Skarpe 1990). However, one has to identify the role of the dominant species in the ecosystem in order to be able to judge the situation. In our case study, the effect of high abundance values for *S. uniplumis* on test site OMA cannot be seen as negative, at least from a farmer's point of view.

Surprisingly, SADs are not often interpreted using the information of rank order of species, but rely mostly on the fit to a specific mathematical model in order to deduce a process from the observed pattern (McGill *et al.*, 2007). We believe that rank order information is crucial for the understanding of the graphs. In case of OMA and NIK-S, the high abundance values of *S. uniplumis,* a valuable fodder species, can be seen as an indicator for good range condition, whereas the high values for *R. trichotomum* on NIK-N indicate a potentially degraded environment. With this example it should become clear that an ecological interpretation of the graphs is incomplete without considering the species involved and model fitting alone might not be sufficient.

An overall comparison between the test sites for the Thornbush savannah and the sites from the Nama Karoo is given in Figure 3. It is obvious that the savannah test sites have higher species richness, higher species abundance values and include more rare species. Why is a comparison like this interesting? It is one of the strengths of SADs to allow comparisons of

totally different ecosystems and to facilitate the visualisation of differences by a graphical solution, which makes the results more obvious and communicable. For example, Hubbell (2001) used SADs to compare diversity patterns of tree species in tropical rainforests with coral reef communities. Murray *et al.* (1999) analyzed the differences in diversity patterns between dry sclerophyll and temperate rain forests, and put an emphasis on differences in the number of tail species. It becomes clear that much less rare species were observed in the drier Nama Karoo than in the Thornbush savannah sites (about 10 on NIK-N and NIK-S versus 50 at OMA and OTJ). However, looking at relative cover values, the difference is not that striking. Overall, species richness of the Nama Karoo sites is lower than of the savannah sites, and the percentage of rare species similar to proportions found in the savannah. Nevertheless, it has to be kept in mind that this can be stated only for the data we have analysed so far and no general conclusions should be drawn from this comparison. Depending on the research question, it can be necessary to also consider environmental factors such as e.g. climate, geomorphology, and management type to allow for valid comparisons of similar ecosystems.

Our intention was to highlight the potential of SADs to allow visual comparisons of different biomes. Interesting questions in this context would be e.g., if the Highland savanna of Namibia, geographically located in between our test sites, would also be intermediate in the SAD plot? Where would test sites from drier areas, e.g. Namib Desert or parts of the Succulent Karoo, line up in the graph, and how would they behave with regard to patterns of dominance and rarity?

Diversity Profiles

The diversity profiles for the Nama Karoo sites (Figure 4) revealed that NIK-S has always higher values for H-alpha than NIK-N, thus it can be concluded that NIK-S is truly more diverse than NIK-N. But the sites do not differ very much in species richness (H_0). The curve for NIK-N starts bending downward at higher values for the scale parameter alpha indicating effects of dominance. Following Kindt (2006), values lower than 0.5 for H-alpha at H_∞ (Berger-Parker index) suggest the occurrence of a species that represents more than 60% of the total abundance. This is true, as we have already seen in the analysis of the species abundance distributions. NIK-S obviously is more evenly distributed, indicating no effects of dominance at H_2 and H_∞. As already mentioned above, this pattern may be due to a more pronounced spatial homogeneity of habitats compared to NIK-N. A similar picture can be revealed for the diversity profiles for OMA and OTJ. Both sites are rather similar according to species richness, but show different patterns for the evenness related indices. Values for H_∞ between 0.5 and 1.5 can still be interpreted as an effect of a dominant species, in this case *S. uniplumis* on OMA.

The comparison of diversity profiles for the Thornbush savannah and the Nama Karoo sites shows an interesting pattern (Fig. 4). The different biomes can be clearly separated according to species richness (H_0). At H_1, equal to Shannon's Diversity, the separation still holds, although the profile for OMA starts to approach similar values found for NIK-S. Looking at the dominance indices (H_2 and H_∞), OMA approaches values close to NIK-N, while OTJ shows

similar values like NIK-S. When talking about evenness, the relation of abundance to the total richness has to be considered. An extremely even profile would be a straight line, therefore we can say that OTJ is not as even as NIK-S, as can be recognized by the overall shape of the two profiles. This arises from the fact that there are much fewer species at the Nama Karoo site. For a final ranking of the test sites regarding biodiversity, it becomes obvious that they cannot be truly ordered by diversity, i.e. profile curves cross each other. Hence, if ranking would be only based on species richness the rank order would be different from an ordering based on Simpson diversity or Berger-Parker Index. However, the test sites can be ordered at least partially, i.e. Species richness and Shannon diversity give the same rank order, while Simpson diversity and Berger-Parker Index show different rank orders. A diversification, e.g. an increase in the evenness, would rely on an increase of the abundances of the less frequent species. However, it should be noted that this data results only from one year and that shapes of profiles might look very different using data from other years.

Interestingly, SADs can help to interpret diversity profiles significantly and *vice versa*. Dominant species, which can be identified by the SAD, tend to decrease evenness in a sample, which can be observed in the diversity profile. To know the value and the ecology of the species that influence the observed pattern helps to understand the pattern of commonness and rarity, which allows a sound interpretation of the diversity of the studied systems. We are not aware of any study that has applied a combination of these techniques.

Interpretation of richness and evenness

There has been a debate on the relationship between richness and evenness components and how to interpret them in relation to ecological processes (Stirling & Wilsey, 2001; Ma, 2005). Following Legendre (1998), a possible interpretation for both aspects can be given: species richness can be interpreted as a function of the stability of an environment. The number of species increases with the availability of realized niches, as provided by a stable environment. By this, both, species diversity and environmental diversity, are considered and can directly be linked. The evenness of the species distribution allows evaluating the overall biological activity of the environment. If there is a low evenness there is a high biological activity, e.g. bush encroached savannah ecosystems show a low evenness due to at least one dominant species. Simultaneously, wood production per unit area increases in comparison to a natural savannah. The reduction of resources, e.g. sustained grazing of a perennial grass sward, can favour the dominance of an increaser shrub species, and thus decreases evenness.

Possible applications

We have shown that the described techniques are powerful tools for comparing biodiversity on different scales, from farm level to ecosystem level. In order to stimulate the usage of these methods we would like to share some ideas for possible applications in rangeland and restoration ecology. They might be useful in order to (i) estimate the effectiveness of restoration efforts aiming at restoring biodiversity, (ii) facilitate monitoring of diversity conditions on rangelands (Lewis *et al.*, 1988), (iii) characterise vegetation states in resilience-based state-

and-transition models (Briske *et al.*, 2008), (iv) describe general patterns of diversity along environmental gradients, e.g. climatic, topographic and temporal gradients, and (v) conduct ecosystems rankings according to the diversity of occurring communities.

Conclusion

With a case study, we have shown, how SADs and diversity profiles can be applied and interpreted in terms of plant species diversity. Although different techniques have already been proposed for diversity ordering (Tóthmérész, 1995, Liu *et al.*, 2007; Mendes *et al.*, 2008), they are still not very well-known in ecology and not much literature can be found on this topic. Diversity profiles allow a logic and straightforward direct visual comparison and interpretation of the most applied diversity indices in ecology at once. Species abundance distribution curves are a simple, yet powerful tool to identify and compare patterns of diversity. A combination of both techniques allows an even better interpretation of the overall diversity pattern. We strongly emphasize the usage of these methods in monitoring and restoration projects. Further, SADs and diversity profiles could become useful in entangling the ecological interpretation of species richness and evenness. However, more empirical studies are needed applying this approach of linking species richness and evenness pattern with special consideration of ecological meaningful plant functions, such as nutritional values, competitive strategies and grazing responses.

Acknowledgements

We thank the editor in chief, Dave Joubert, as well as Joh Henschel and one anonymous reviewer for their valuable comments on the manuscript. We further thank the local farmers for their permission to work on their land and for the information they shared, as well as the Namibian Ministry of Environment and Tourism for granting the research permit. Furthermore, we thank all the students who helped in gathering the data on the test sites and the German Federal Ministry for Education and Research (BMBF) for funding under promotion number 01 LC 0024A.

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