POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	49	1	91–94	2001
Short contribution				

Werner ULRICH

Nicholas Copernicus University in Toruń, Department of Animal Ecology
Gagarina 9, 87-100 Toruń; Poland, e-mail: ulrichw@cc.uni.torun.pl

ON THE SCALE DEPENDENCE OF EVENNESS

ABSTRACT: A recently reported (Wilson *et al.* 1999) effect of spatial scale on evenness is studied and it is shown that such a pattern is not necessarily an effect of changes in community structure at different scales but may simply result as a by-product from constraints introduced by maximum and minimum allowed densities due to the sampling procedure. Evenness is found to be constant only if the species area relationship of the community under study has exactly the parameter values that are given by the parameter values of the relative abundance distribution of the community. Because such a situation will seldom occur under natural circumstances scale dependence of the evenness (and of related descriptors of structure) is expected to be a general feature.

KEY WORDS: Evenness, random assortment, species-area relation, relative abundance distribution, spatial scale

In the last years the effects of spatial scales on community structure and macroecological patterns came more and more into the focus of interest (Wiens 1989, Collins *et al.* 1993, Palmer and White 1994, Wilson *et al.* 1998, Ulrich 2000). Recently, Wilson *et al.* (1999) reported that the evenness of plant communities (measured by three different indices which are independent of species number) is not constant but decreases at larger scales. They sampled six plant communities at dune slack sites and semi-arid grasslands and found a logarithmic dependence of evenness on spatial grain at scales from 1 to 25 m of quadrate length. From random samples out of a geometric distribution that served as a null model they expected rather the opposite trend, an increase of evenness at larger spatial grain.

Because the evenness is closely connected to other aspects of community structure such as diversity, relative abundance distributions, species-area relations or stability, the above findings have broader implications for comparisons of communities from different spatial grains. It is therefore worthwhile to look closer at them.

The authors interpret their results as stemming from intrinsic frequency/abundance patterns or from patterns produced by environmental variation and speculate that their finding will be one of the few general rules in community ecology.

However, the effect may also be simply a byproduct resulting from the sampling procedure. In the following I will show that constraints by upper and lower possible densities in samplings may produce a similar pattern than found by Wilson *et al.* (1999) and that this pattern then is an outcome of ordinary species-area relationships.

Wilson *et al.* (1999) treat their samples as whole communities, a way which is probably correct for plant communities but may be questionable in the case of animals. However, adopting this concept we do not have to worry about missing species and can treat each sampling area as a whole.

Generally, relative abundance distributions are drawn without referring to upper and lower limits of density. However, this is not correct and in this special case we have to look especially at lower possible densities. Imagine sample quadrates of 1 to 625 m^2 area [as in the study of Wilson *et al.* (1999)]. If we now place S species each in these quadrates their densities will range between the upper possible density for each quadrate (determined by environmental conditions) and the lower possible density, given as the reciprocal of quadrate size. At larger quadrate size the upper density limit will of course remain constant, the lower possible density will decrease. Let us for simplicity assume that the species are distributed according to a random assortment distribution (which is most often found at smaller sample sizes). In this case we reach at a picture like in Figure 1. The evenness (given by the slope of the log (abundance)-species rank order plot will systematically decrease at higher sample areas simply because the species will be able to fill a larger density range. If we take the common index E derived from the information measure H of diversity we find a logarithmic dependence of E on area (Fig. 2) very similar to the pattern found by Wilson *et al.* (1999).

More interesting is of course the case when the species number rises at larger areas according to a species-area relationship. If we again assume a random assortment relative abundance distribution we see that the evenness will be constant only if the log (abundance)-species rank order plot has the same slope at different minimum densities (Fig. 3). The minimum densities are again the reciprocals of the quadrate size. Therefore we can reformulate the relative abundance distribution in terms of area sampled:

$$\ln\frac{1}{D}-\ln\frac{1}{D\times area}=k\left(S_2-S_1\right) \qquad (1)$$

with D and S_1 being the maximum densities and the species number at quadrate size 1, area and S_2 the area and species number of the largest quadrate size, and k the slope of the distribution. Equation 1 results after simple rearrangement into a description of the required species-area relationship for constant evenness:

$$S_2=S_1+\frac{1}{k}\ln\left(area\right) \qquad (2)$$

This is of course the well known exponential species-area relationship known to follow from a log-series or geometric distribution (of which the random assortment is only a stochastic counterpart) (Pielou 1977, Tokeshi 1993). The evenness of a community according to a random assortment or

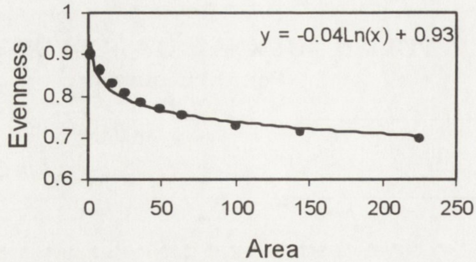

Fig. 2. Evenness in dependence of sampling area assuming a pattern as in Fig. 1.

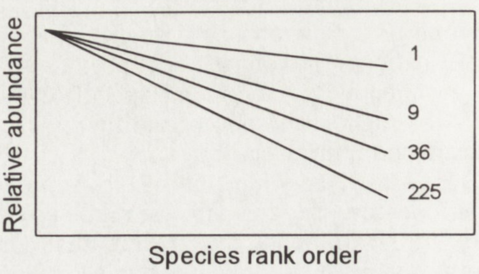

Fig. 1. Shapes of 4 random assortment relative abundance distributions with the same number of species but increasing minimum allowed densities due to increasing sampling area. If the species fill the whole range of allowed densities the slope of the distribution will rise resulting in a decrease of evenness.

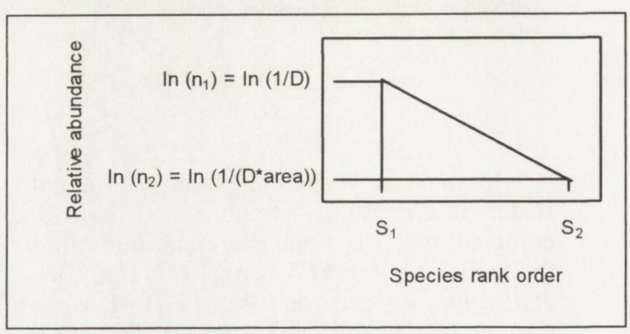

Fig. 3. Relative abundance-species rank order plot of a random assortment distribution with relative abundances n_1 and n_2 and species numbers S_1 and S_2 at quadrate size of 1 and quadrate size of *area*. D – maximum allowed density per quadrate.

log-series model sampled at different scales will therefore only be constant if the factor is exactly the reciprocal of the slope (=1/k) of the log (abundance)-species rank order plot. This is a quite improbable situation and under most circumstances evenness will not be constant but vary.

Wilson *et al.* (1999) found that the evenness in all of their study sites decreased. To see why this is probably the most often found type we have to look closer at the relationship between S_1 and k. Unfortunately, nearly all species area relationships are given in power function form and it is convenient to reformulate equation 2 into a power function species area relation. After equating equation 2 with the power function $S_a = S_1 area^z$ we get after simple rearrangement:

$$z \approx \frac{\ln\left(1+\frac{1}{k \times S_1}\ln(area)\right)}{\ln(area)} \qquad (3)$$

At small scales this relation is largely area independent and we can plot the slope z in dependence of k and S_1 (Fig. 4). Because most natural communities have z-values below 0.3 (Connor and McCoy 1979, Rosenzweig 1995) a constant evenness is then expected only if the community has a very unequal relative abundance distribution (much more uneven than for instance a lognormal). More equal distributions would inevitably require high slope values of the species area relation. Relative even distributions together with species-area relations with slopes below 0.3 result in a decreasing evenness at larger scales if the species number per

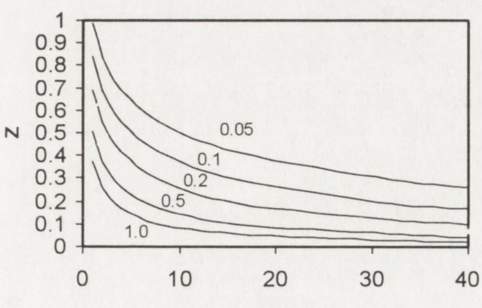

Fig. 4. Slopes z of the power function species-area relationship in dependence on the species number at quadrate size 1(S_1) and the slope k (values given) of the random assortment distribution in a log (abundance)-species rank order plot as defined by equation 3.

sample quadrate is small. At higher species numbers per sample quadrate the evenness is expected to increase.

Wilson *et al.* (1999) reported species numbers S_1 from 5 to 10 species and from a previous paper of the same authors (Wilson *et al.* 1998) it is possible to estimate the slope values at all of their sites: 0.13 to 0.2 for the slack sites and 0.16 an 0.23 for the grasslands. Under this conditions Figure 4 points clearly to a decreasing evenness at larger scales as found by Wilson *et al.* (1999).

Evenness is only one aspect of community structure and is closely related to other features like diversity or type of relative abundance distribution. The basic feature seems to be the latter and together with environmental constraints it determines the species area relation. Defining species assemblages in terms of sample units introduces new constraints both into species-area relations and relative abundance distributions. These new constraints do not effect the distributions but the distribution measures and result inevitably in some scale dependence. With the same arguments as above it is possible to infer the scale dependence of diversity or relative abundance distributions. A scale dependence of the latter will also result in a scale dependence of the accompanying species-area relationship, a pattern that had already been reported by Palmer and White (1994).

The above argument does not mean that there are no scale dependencies beside the once introduced due to sampling. However, sampling effects have to be considered when studying communities at different scales and basic features like species-area relations have to be studied parallel.

Nevertheless, the work of Wilson *et al.* (1999) brings one problem into focus which had previously been widely neglected. Diversity and evenness measures are often used to compare communities. It may be that differences found are not due to changes in community structure but are simply a consequence of the species-area relationships of the taxa or guilds under study. It would be worthwhile to compare community structure and species-area relations at the same time to distinguish between these possibilities.

ACKNOWLEDGMENTS: I thank Prof. J. Buszko and Dr. Kartanas for critical and valuable suggestions on the manuscript.

REFERENCES

Collins S. L., Glenn S. M., Roberts D. W. 1993 – The hierarchical continuum concept – J. Veg. Science, 4: 149–156.

Connor E. F., McCoy E. D. 1979 – The statistics and biology of the species-area relationship – Am. Nat. 113: 791–833.

Palmer M. W., White P. S. 1994 – Scale dependence and the species-area relationship – Am. Nat. 144: 717–740.

Pielou E. C. 1977 – Mathematical Ecology – John Wiley & Sons (New York).

Rosenzweig M. L. 1995 – Species diversity in space and time – Cambridge, Univ. Press.

Tokeshi M. 1993 – Species abundance patterns and community structure – Adv. Ecol. Res. 24: 111–186.

Ulrich W. 2000 – On species–area relationships III: The intercept of the power function and the exponential model – Pol. J. Ecol. 48: 37–48.

Wiens J. A. 1989 – Spatial scaling in ecology – Funct. Ecol. 3: 385–397.

Wilson J. B., Gitay H., Steel J. B., King W. McG. 1998 – Relative abundance distributions in plant communities: effects of species richness and of spatial scale – J. Veg. Science, 9: 213–220.

Wilson J. B., Steel J. B., King W. McG., Gitay H. 1999 – The effect of spatial scale on evenness – J. Veg. Science, 10: 463–468.

(*Received after revising March 2000*)