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Species diversity: a personal retrospect

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Eddy van der Maarel, an Honorary Member of the International Association for Vegetation Science, recently celebrated his 80th birthday. Eddy is a founding editor of *Journal of Vegetation Science and Applied Vegetation Science*, currently our main arena for plant community studies. Eddy has been a mentor, teacher and close friend for a large number of plant community ecologists, which he has often called family. Many of us have benefited from his support, especially during those difficult times when the world was divided by the Iron Curtain. Very few other scientists have served our society so greatly. Eddy has been in vegetation science for more than a half century and he has worked on very many topics. In his Guest Editorial he provides a personal view on species diversity, a topic to which he has made perhaps the strongest contribution. We wish to Eddy good health and promise to keep in close contact to discuss not only science, but also music, languages or gardening.

On behalf of hundreds of vegetation scientists, the Chief Editors.

This essay attempts to follow the development of the concept of species diversity from the time before this concept was coined up to the present. The choice and subsequent use of diversity indices will be briefly discussed as to their usefulness for vegetation ecology. Here, the emphasis will be on plant diversity. My own involvement in this theme spans almost exactly 50 yr now and therefore this retrospective is personal.

The first notion of species diversity stems from inventories of species in series of individuals or different areas that were compared with each other. Most early counts of species are zoological. In particular, moths and other insect species have been investigated in samples of individuals. Early examples have been discussed by Williams (1964). The entomologist Williams does not seem to have been fully aware of early botanical studies of species numbers and area and variation in abundance. Thanks to Du Rietz (1921) I became aware of the pioneer studies of Von Post (1851), who compared species richness values of similar

landscapes of different size and developed almost certainly the very first abundance scale, with six values, ranging from very rare to very frequent. For comparison, a Dutch pioneer, Holkema (1870), used a four-point scale, ranging from, in modern terms, dominant, to abundant, locally abundant and rare, for the species occurring in the vegetation on the Dutch Wadden Islands. He appears to have been aware of the relationship between number of species and area of the Dutch Wadden Islands. He was also explicitly aware of the relationship between habitat and species diversity, albeit without using the terms.

Through Fig. 2.1 in the well-known book of Rosenzweig (1995) I started to study the work of the famous botanist A.L. Watson. Rosenzweig called this figure the ‘first species–area curve (Watson 1859).’ I had earlier overlooked this figure. I should add that according to Rosenzweig it was Williams (1964) who credited Watson with its discovery in 1859. I became somewhat suspicious, because I was sure that Williams (1964) did not credit Watson, although

he used data from Watson (given on p. 315 of his book), which he included in his Fig. 38, pp. 94–95. Williams (1943) did refer to Watson (1859), but there he mentioned other data from Watson.

Let me first add that the 1859 publication of Watson was volume IV of his four-volume magnum opus, which was published from 1847 to 1859 under the curious main title '*Cybele Britannica*', after the goddess Cybele, who is known, among other things, as the mother goddess of earth and life. Rosenzweig (1995) also mentioned a study by Dony (1963) on species–area relations in Hertfordshire, in which Dony referred to an earlier quotation from Watson (1835), which I copy: 'on the average a single county appears to contain nearly one half the total number of species in Britain; and it would, perhaps, not be a very erroneous guess to say that a single mile contains half the species of a county.' Dony, apparently knowing about the later data from Watson (but referring to the wrong volume), assumed that the county must have been Surrey (although he gave 1000 quadrat miles as the mean county area, which is much more than the area of Surrey). Anyway, Dony presented a log-log graph with three approximate area sizes and species numbers and roughly obtained a straight line (his Fig. 6). He concluded that Watson was 'very near to the truth,' i.e. of discovering the log-log species–area relationship. Finally, a paper from Triantis et al. (2003), apparently following Rosenzweig (1995), concluded: 'However, there is no doubt that the first plot relating species with area, was made by Watson in 1859.' Here, they refer to Williams (1964) who, as I said, did not credit Watson (1859). Dony (1963) was of the same opinion, but he again did not refer to Watson (1859), while Triantis et al. refer to a graph which was never developed by Watson, but by Rosenzweig.

Table 1. Species counts of nine nested areas from 1 mile² in Surrey to the whole of Britain, according to Watson (1859), p. 381. Note that the total area of All Britain, England and Surrey deviates from actual data. Watson added two columns to this table, one with square mile area divided by species number, and one with species number per 10 mile². Apparently Watson wished to emphasize the regular relationship between the two parameters.

	Area in mile ²	S
All Britain*	87412	1425
England**	57812	1350
S Britain	38474	1280
Province Thames	7007	1051
South part Thames	2316	972
Surrey***	760	840
60 mile ² Surrey	60	660
10 mile ² Surrey	10	600
1 mile ² Surrey	1	400

*Nowadays 93800, **50346; ***642 mile².

Despite these inaccurate interpretations it is clear that Watson (1859) was indeed impressively near to the idea of a species–area relation, but not as near as some of the above-mentioned authors stated. Fortunately the four-volume magnum opus of Watson appeared to be available digitally and I could reconstruct the situation. As an aside: Williams (1964) used only data from eight of the nine areas, and so did Rosenzweig. Data on area and species number have been copied from p. 381 in Watson (1859). Watson explicitly made clear that the nine areas he included in the comparison are nested. There are many more data of this kind listed in the book, but these nine are introduced as 'series'. In what we may consider as the first attempt to relate species number to area, Watson presented the relationship between species number and area in four columns, two of which are presented in Table 1. Watson deliberately put the largest area first and added the following comment, 'A rapidly decreasing area with a less rapidly decreasing species number.' So, he was clearly aware of some sort of relationship between species and area, which also follows from the two columns in his table. However, it would go too far to consider him as the inventor of the log-log relations.

This is not the end of the Watson story. There is more of special interest in this volume IV of Watson. I discovered that on p. 436 he remarked that two 'tracks' (let us say samples) may be similar regarding their flora, but probably there will be 'inequality of frequency' between the samples, meaning differences in abundance. Here he introduced the term 'vegetal diversity' and it seems that it was meant to refer to differences in abundance. All the more fascinating is the introduction (p. 427) of the term 'floral diversity'; it has not become clear how he calculated it, but conceptually it is the difference between two 'floras', let us say species lists; if list A has species which are missing in a list B, this is an element of 'positive diversity' for A, while the absence of species in A which occur in B, is 'negative diversity'. An exact calculation seems to be missing, but it is again a germ, in fact a precursor of the concept of dissimilarity among samples as a measure of diversity. Anyway, floral diversity looks like a design of a β -species diversity measure.

In the 1930s and 1940s Williams (1944, 1964) described the relationship between number of species and number of individuals (animals) with the logarithmic series (Fisher et al. 1943). In a simplified form it describes the cumulative increase in the number of species as a function of the logarithm of the cumulative number of individuals: $(S_2 - S_1) = \alpha (\ln N_1 - \ln N_2)$. Plotting S against $\log N$ results in a straight line that often fits the series of points well over a larger part of the graph. The value of α is a measure of the rate of species accumulation with increasing size of the sample. Williams (1964) also described relationships

between the number of plant species and the number of small quadrats in which they were observed. He included data from O. Arrhenius, but he seems to have missed the work of this author and his contemporaries Romell (1926) and Kylin (1926), who all worked with species counts on small quadrats, which could be included into larger areas. Arrhenius (1918, 1920, 1921) found for his small quadrats a double logarithmic relation: $(\ln S_2 - \ln S_1) = z (\ln A_1 - \ln A_2)$, with S = number of species and A = area. The result was criticized by Gleason (1922), who made clear that extrapolation of Arrhenius' results to much larger areas would result in unrealistically high species numbers. He made a similar study and found a good fit using the semi-logarithmic approach. Romell (1926) came to the same conclusion and suggested the semi-logarithmic approach for small areas. I applied all three relationships (Van der Maarel 1966) and found, indeed, that for smaller (grassland) areas the semi-log relationship was more realistic.

The Arrhenius equation was elaborated much later by Preston (1962) on the basis of a truncated log-normal distribution of individuals over species (he used the term 'Arrhenius equation'). The equations Preston developed, for complete collections of different size and of samples, for numbers of individuals and areas, can be reduced for the species–area relationship as given in the Arrhenius equation. The value z was calculated as 0.28 for complete collections. Kylin (1926) proposed an asymptotic function $S = \Sigma S (1 - e^{-cA})$, where S and A are as above, ΣS is the total number of species involved, c is a constant and e is the base of the natural logarithm. This relationship is typically realistic in the case of a very homogeneous vegetation type in an extreme environment such as a salt marsh. Interestingly, the concept of minimal area, which has been a concept without an accepted analysis, is wrongly determined on the basis of a linear–linear plot of S against A , which is in most cases misleading (e.g. Van der Maarel 2005).

Perhaps we should consider Gleason as the originator of the semi-logarithmic species–log area relation, and Arrhenius as the originator of the double-logarithmic relation. Williams (1964) concluded that his logarithmic series was generally applicable to smaller samples, say within a community. In my own (small-scale) grassland analyses (Van der Maarel 1966), the semi-logarithmic relation was the best fit. For larger samples and areas the log-log model of Arrhenius and Preston was considered more appropriate. However, for larger samples the 'law of the large numbers', becomes real (May 1976): 'once a community consists of a relatively large and heterogeneous assembly of species, the observed distribution of species relative abundances is almost always lognormal.'

From the beginning of the study of species–area relations there has been a notion of the unequal number of

individuals belonging to a species, and the experience that in species-rich samples most species are represented by very few individuals. Botanists have been aware of the differences in abundance of species, and according to new discoveries in the literature, this notion arose as early as around 1850. Simpson (1949) is probably the first to have developed a measure of this inequality: $\lambda = \Sigma p_i^2$, where p_i is the proportion of species i ; this is the weighted mean of proportional abundances. Whittaker (1965) is probably the first to have realized that species usually differ in abundance in a consistent manner. He developed the concept of the dominance–diversity curve in which the species abundance is plotted on the y -axis and the species are arranged along the x -axis according to their decreasing abundance. Whittaker also concluded that species with a high abundance determine, to a large extent, the value of λ ; in the extreme case of one species approaching full dominance, λ approaches 1. Hence the index is rather an index of dominance, which is in line with Simpson's own term: index of concentration. A similar index, based on information theory, is $H' = -\Sigma p_i \ln p_i$ (Shannon & Weaver 1949), which was introduced into ecology by Margalef (1951; see Margalef 1968). These indices are called α -indices, with reference to the α of Williams. Whittaker (1972) has introduced two higher levels of diversity: β -diversity as a mean dissimilarity between community samples in the same area, particularly along gradients, and γ -diversity as species richness in larger landscape units.

The various indices mentioned above and further variants have been used throughout the period since their introduction. In a first comprehensive survey of species diversity measures, Peet (1974) described many variants of the above-mentioned measures, and summarized comments on the appropriateness of indices in relation to the underlying model of variation in species abundance and the completeness of samples. Peet also included the interesting approach presented by Hill (1973), which he derived from Rényi (1961), who defined a generalized entropy with different orders. When applied to species abundance relations, the general equation is $N_a = \Sigma p_i^{a/(1-a)}$ where N_a is 'diversity of order a ', with a varying from $-\infty$ to $+\infty$. Three 'orders' N_a lead to well-known indices: N_0 = number of species; N_1 = exponential Shannon index; N_2 = reciprocal of the Simpson index. The survey of indices by Anne Magurran (1988) concentrated on the coherence between diversity indices and species abundance models. She treated the Shannon index as a diversity measure and the Simpson measure as an index of dominance.

Rosenzweig (1995) showed that in larger samples the double-logarithmic Arrhenius–Preston relation is usually the best fit. The z -values vary around the theoretical value, but for sets of smaller (partial) areas z -values may be much lower, and values of sets of islands are usually higher than

comparable sets from mainland areas. A special case is the log-log species–area relation for the entire Netherlands, with 1357 species ($z = 0.28$), which is used to judge the position of individual nature reserves and regions (Van der Maarel 1971, 1997).

I suggested (Van der Maarel 1997) that the two diversity indices, α and z , resulting from species–area curves, are important indices because they can be estimated relatively easily. They can also be used when no accurate data on the abundance of species are available. Of course, the distribution of abundance values is a very interesting characteristic in its own right. However, I do not consider abundance of species an important aspect of diversity, but rather of the structure of a plant community. We know that many species-rich communities often contain many rare species. Here it should not make any difference in the importance of such communities how significant differences in the abundance of the abundant species are. The dominance–diversity curve developed by Whittaker is a useful graphic way to combine species richness and dominance, e.g. for the description of an old-field succession (Whittaker 1972; his Fig. 3). In my opinion, species richness is the central diversity measure. Of course, richness should be compared on areas of the same size. Studies of species richness S on standardized areas including 1 m², 10 m² and 100 m² for small-scale analyses and 0.1 and 1.0 ha for larger-scale analyses may give ecologically interpretable results. There are numerous plots of the same size, with species counts, and often the environmental data are available in many databases. If there is a sampling constraint (too few plant units), a temporal component can be included (Fridley et al. 2006). An old example of species richness per m² against a local microgradient showed how highest richness occurred at places with intermediate pH (Van der Maarel & Leertouwer 1967).

In addition to area, habitat heterogeneity is extremely important. As an example, the species richness of the Frisian Wadden Islands (Van der Maarel 1981) showed a log-log relationship with the area of the islands, but some islands deviated. Van der Maarel (1997) compared the position of these islands on a graph of the log S –log A relation with the number of habitat types (based on physiographic characteristics) per island. For the sandy islands with dunes, the log S –log A relation was significant ($z = 0.256$). On the whole, the habitat diversity increased significantly with island area. However, the smaller islands with a simple structure and with few habitat types were poor in species and hardly showed a species–area relationship.

This concludes my essay. A next step would be a discussion of the application of species diversity measures to actual ecological issues, within the broader framework of biodiversity.

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