

Werner ULRICH

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

SPATIAL SCALING LAWS AND WEIGHT DEPENDENT DISTRIBUTIONS IN GUILDS OF DIPTERA AND PARASITIC HYMENOPTERA

ABSTRACT: This paper tests the recent published synthetic theory of biodiversity of Ritchie and Olff (1999) using data on parasitic Hymenoptera and soil living Diptera. Neither the predicted size dependent size ratio patterns, nor the left skewed species number-size class ratios, nor right skewed species richness-productivity patterns were found. It is concluded that the basic assumptions of the theory (self similarity of habitat, food, and resource distribution over ecological relevant scales) is not applicable at fine scales and to guilds of higher trophic levels. Whether in general the assumptions are applicable to plants and phytophages has to be decided by further studies.

KEY WORDS: Spatial scaling laws, Hymenoptera, Diptera, diversity, niche, resource acquisition

1. INTRODUCTION

Recently, Ritchie and Olff (1999) developed a synthetic theory of biodiversity assuming simple scaling principles of resource acquisition. Starting with the notion that species of different size divide up space and therefore resources in a different manner and using fractal geometry they derived rules describing relationships between available niche space, productivity, area, and body size for guilds of species of similar resource requirements.

Under the hypothesis that the distribution of (in their terms) habitat, food, and resources is nested and statistically self similar

across ecologically relevant ranges of scale the fractal dimensions D , F , and Q of habitat, food, and resource distribution are described by $D \geq F \geq Q$. Relating patch size (P) and resource concentration (R) to these fractal dimensions resulted in two basic scaling laws:

$$P_i = (L/mkr)^{1/2} w^{(D-Q/2)} \quad (1)$$

$$R_i = (Lr/mk)^{1/2} w^{(Q/2-F)} \quad (2)$$

with P_i and R_i being the threshold patch size and resource concentrations for coexistence of species, m and r the local densities of food and resources, L the resource loss rate, k the number of habitat subvolumes, and w the variable of interest, for instant body length, weight, area, or productivity.

The above model results in three main predictions: Minimum size ratios of morphological parameters (larger/smaller species), for instance body weight or body length ratios, that allow coexistence of species are not constant but are size dependent, plots of species richness versus size class (species-weight distributions, SWD) should be unimodal and left skewed, and plots of species richness versus productivity should also be unimodal but right skewed (Fig. 1).

However, if the model holds it will have implications on other basic ecological distributions as well. Harte *et al.* (1999) already showed that the concept of self-similarity leads to power function species-area relationship and the same relation can be derived

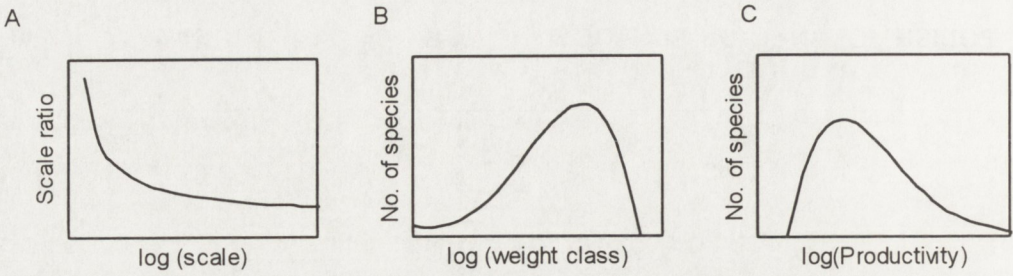


Fig. 1. Scaling laws predicted by the model of Ritchie and Olff (1999). A: Size ratios versus size of the larger species; B: Number of species in a guild of similar resource requirements versus log (size class) of the species; C: Number of species in a guild of similar resource requirements versus log (habitat productivity).

from Ritchie and Olff's model. Ulrich (1999b) found that unimodal right skewed (log-normal) or normal (symmetric) species-weight distributions together with ranges of species density fluctuations that are weight dependent (density-weight distribution DWD) result in unimodal (left- or right-skewed or symmetric) or increasing biomass-weight distributions (BWD), contrary to the popular equal biomass hypothesis (Damuth 1981) but in accordance with the findings of Strayer (1986), Maurer and Brown (1988) and Stork and Blackburn (1993) (Fig. 2A). A higher variance in the DWD results in bimodal or even in multimodal BWDs (Fig. 2B). Left skewed SWDs, as predicted by Ritchie and Olff, will nearly always result in left skewed unimodal BWDs or bimodal distributions with the highest biomass in the upper weight classes (Fig. 2A),

but not in linear rising or right skewed distributions.

Ritchie and Olff tested their model using communities of Minnesota plants and of East African herbivores and found good agreement of the data and the model. These are guilds of the first and second trophic level. The model requires guilds of similar resource use but most published data on species numbers that also include data on weight and size ratios deal with rather heterogeneous assemblages for which the model not applies.

For the present test of the model I chose arthropod guilds of similar resource and habitat requirements of the second and higher trophic levels of two habitats: parasitic Hymenoptera in a forest (Ulrich 1998) and parasitic Hymenoptera and soil living saprophagous and predatory Diptera in an open landscape habitat (Hövmeyer 1996, Ulrich 1999a).

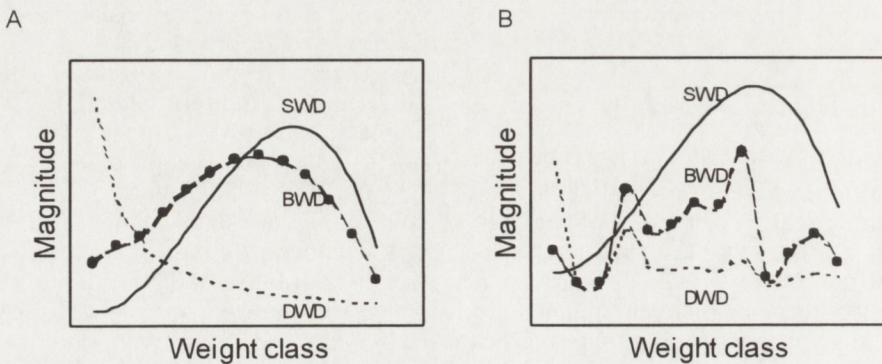


Fig. 2. Relationships between species-weight distribution (SWD), density-weight distribution (DWD), and biomass-weight distribution (BWD). A: combining a SWD with a strict DWD (that is a DWD with a correlation coefficient of 1 as in A) results always in a unimodal BWD; B: a higher variance of the DWD (a correlation coefficient less than 1 as in B) causes bi- or even multimodal BWDs (for details on this relation and computation procedures see Ulrich 1999b). Magnitudes: for SWD: species; for DWD: log (densities), for BWD: total biomass (mg/m²) per weight class.

2. MATERIALS AND METHODS

This paper uses data on species numbers, densities and body weights of hymenopteran and dipteran guilds obtained in two habitats on limestone in northern Germany, a beech forest (Melico Fagetum) and a dry meadow (Gentiano Koelerietum). Study sites, species composition and density and biomass data have already been published in detail (for Hymenoptera: Ulrich 1988, 1998, 1999a; for Diptera: Hövemeyer 1985, 1992a, 1996).

For oligo- or polyphagous parasitoids the equivalent of habitat productivity is the number of hosts available in a food web. The third prediction of Ritchie and Olff may therefore be tested by plotting parasitoid species numbers and host densities from the same food webs. Such comparisons were possible using the results of breeding experiments of parasitoids of necrophagous Diptera out of dead snails. Out of a total of 147 snails (*Arion ater*) exposed in summer 1986 10 braconid and diapiiid parasitoid species emerged from 4 dipteran host species. Detailed descriptions of the experiments, the species bred and the food web contains Ulrich (1999b).

A second test uses samplings of parasitic Hymenoptera from long term experiments with a manipulated (enhanced and reduced) amount of leaf litter in the beech forest (Hövemeyer 1992b, Ulrich 1999c). Data from 4 years (1983 to 1986) of plots with an initial 5 fold amount and of plots with continuous litter-reduction resulted in a gradient of leaf litter and different host densities for parasitoids of soil inhabiting dipteran host larvae (data on Diptera from Hövemeyer (1992b), on Hymenoptera from Ulrich (1999c). Again parasitoid species number and host densities are compared.

Body weight and total biomass was computed according to the regression method in Ulrich (1998) using the equation

$$DW[mg] = 0.52493 \times V \left[\frac{mg}{mm^3} mm^3 \right] \quad (3)$$

with DW being the individual dry weight and V the thorax volume given as the product of length of thorax and propodeum \times max. height of thorax \times width of mesoscutum. Body weight ratios are computed by dividing the dry weights of the larger through the dry weights of the smaller species after ranking the species according to their body weights.

For computing density-weight and biomass-weight distributions see Ulrich (1999b, d). Weight ratios were obtained after ranking the species according to body weight. Skewness (S) of the distributions was computed using the third central moment with

$$S = \frac{n}{(n-1)(n-2)} \frac{\sum_{i=1}^n (x_i - \mu)^3}{\sigma^3} \quad (4)$$

with n being the number of classes and x_i , the values per class, μ the mean and σ the standard deviation of the distribution. Deviation from normality was tested with the Shapiro-Wilk test implemented in the STATISTICA software package.

3. RESULTS

3.1. WEIGHT RATIOS VERSUS BODY WEIGHT

Figures 3 and 4 show the weight ratios of 19 guilds of parasitic Hymenoptera of the beech forest and the dry meadow. In none of the cases a negative dependence of ratio on body weight appeared. However, especially in the forest data a different pattern came up. Upper and lower weight classes have larger weight ratios than intermediate ones. A simple method to show this pattern is to divide the range of weight classes into three parts, upper, lower, and intermediate classes (Table 1). 6 out of 10 mean ratios of the upper weight classes and 7 of the lower weight classes are significantly (one sided t-test: $p(t) < 0.05$) higher than the ratios of species of intermediate weight classes. This gives the plots of Figure 3 a V-shaped appearance. On the dry meadow this trend is less obvious. In 5 of the guilds the upper and lower weight classes have higher weight ratios ($p(t) < 0.10$) than middle ranking species.

3.2. SPECIES AND BIOMASS-WEIGHT DISTRIBUTIONS

Table 2 gives the skewness of the species-weight distributions of all dipteran and hymenopteran guilds studied. All distributions appeared to be distinctly unimodal (data not shown), 13 of them are right-skewed, 5 left-skewed and 6 can be described by a normal distribution. In the beech forest

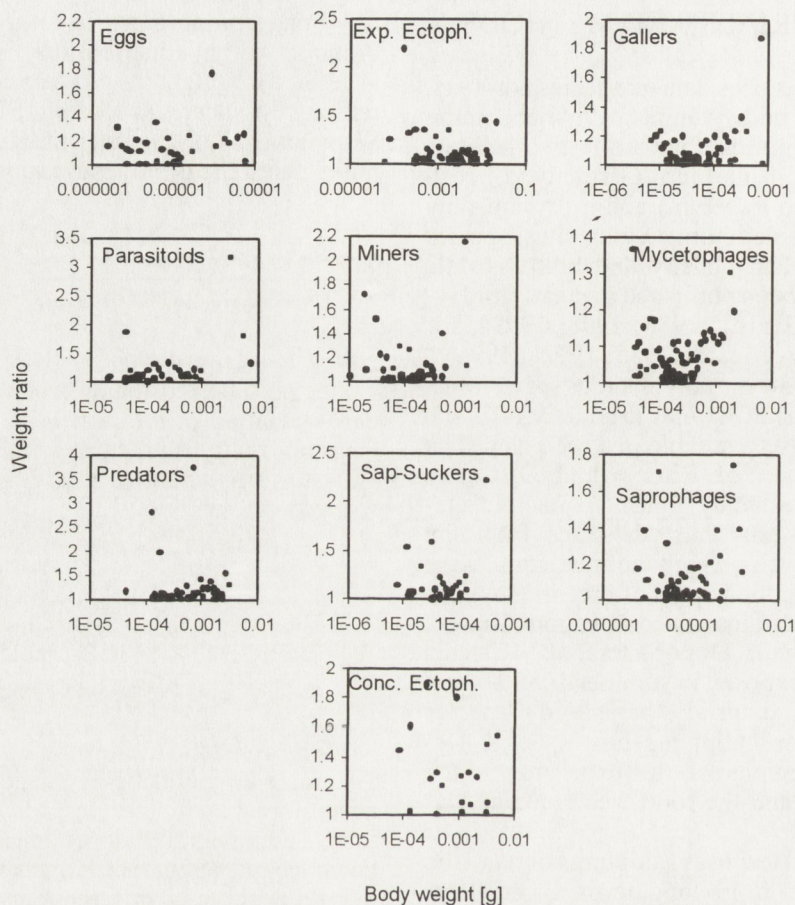


Fig. 3. Weight ratios (body weight of larger/smaller species) against body weight of the larger species (after ranking the species according to their body weight) for ten guilds of parasitoids (host given) of the beech forest.

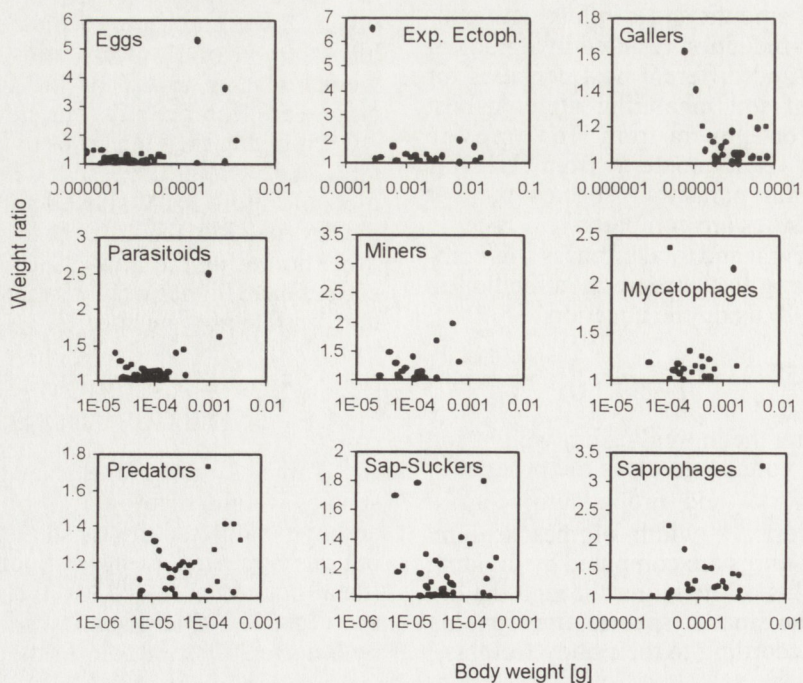


Fig. 4. Weight ratios (body weight of larger/smaller species) against body weight of the larger species (after ranking the species according to their body weight) for nine guilds of parasitoids (host given) of the dry meadow.

Table 1. Significance values of one sided t-test (different variances) of differences in mean size ratio between lower and median and upper and median third of logarithmic weight classes of guilds of parasitic Hymenoptera

Parasitoids of	Beech forest		Dry meadow	
	upper third	lower third	upper third	lower third
Eggs	0.01	0.04	0.06	0.07
Exp. ectophytophages	0.009	0.04	> 0.1	0.14
Gall-makers	0.02	0.009	0.14	0.04
Parasitoids	> 0.1	> 0.1	> 0.1	> 0.1
Miners	> 0.1	0.03	0.04	0.09
Mycetophages	0.004	0.009	0.08	0.09
Predators	0.03	> 0.1	> 0.1	> 0.1
Sap-suckers	> 0.1	0.04	> 0.1	> 0.1
Saprophages	0.02	0.05	0.03	0.04
Conc. ectophytophages	> 0.1	> 0.1	-	-

Table 2. Number of right- or left-skewed species-weight class distributions of 19 parasitoid and 5 dipteran guilds (more than 20 species) of a dry meadow and a beech forest. All distributions are distinctly unimodal. Guild composition of Hymenoptera as in Ulrich (1998, 1999a), of Diptera as in Hövemeyer (1996)

Habitat	Taxon	Right-skewed	Left-skewed	Not skewed
Beech forest	Hymenoptera	4	3	3
Dry meadow	Hymenoptera	5	2	2
	Diptera	4	0	1
Sum		13	5	6

left skewed are the parasitoids of ectophytophages (concealed and exposed hosts) and the parasitoids of miners, on the dry meadow again the parasitoids of (exposed) ectophytophages and parasitoids of gall-makers. In both arthropod groups no preponderance of left-skewed distributions, as predicted by Ritchie and Olff (1999), occurs.

Left skewed species weight-distributions should result in biomass-weight distributions that accumulate the highest biomass in upper weight classes (Fig. 2). Table 3 shows that in 9 of the dipteran and hymenopteran guilds middle and lower weight classes accumulated more biomass than upper weight classes. The opposite pattern was detectable in only 11 guilds. In the forest this again is the case for both guilds of parasitoids of ectophytophages and for the parasitoids of miners. On the dry meadow 6 out of 9 parasitoid guilds accumulated more biomass in upper weight classes. Exceptions were the egg-parasitoids and the parasitoids of miners and gall-makers. In the Diptera zoophages and zoosaprophages accumulated more biomass in upper weight classes.

3.3. SPECIES-PRODUCTIVITY DISTRIBUTIONS

To detect the dependence of parasitoid species numbers on host density, sampling results from experimental plots with a manipulated amount of leaf litter were taken. For comparison only soil living parasitoids were taken for which hosts densities are available. Figure 5 shows that for host densities ranging over 2 orders of magnitude parasitoid species numbers (parasitoids of mycetophages and of saprophages) and log (host densities) are linearly related.

The same result appeared when comparing parasitoid species numbers and host densities from breeding experiments using dead snails as feeding substrate (Fig. 6). Host densities ranging over nearly 3 orders of magnitude did not show the unimodal right skewed distribution predicted by Ritchie and Olff but again a linear dependence of species number on log (host density).

Table 3. Number of right- or left-skewed biomass-weight class distributions of 19 parasitoid and 5 dipteran guilds (more than 20 species) of a dry meadow and a beech forest. Guild composition of Hymenoptera as in Ulrich (1998, 1999a), of Diptera as in Hövemeyer (1996)

Habitat	Taxon	Unimodal			Bimodal	
		Right-skewed	Left-skewed	Not skewed	Max. biomass in lower weight classes	Max. biomass in upper weight classes
Beech forest	Hymenoptera	3	2	3	1	1
Dry meadow	Hymenoptera	1	3	1	1	3
	Diptera	0	0	0	3	2
Sum		4	5	4	5	6

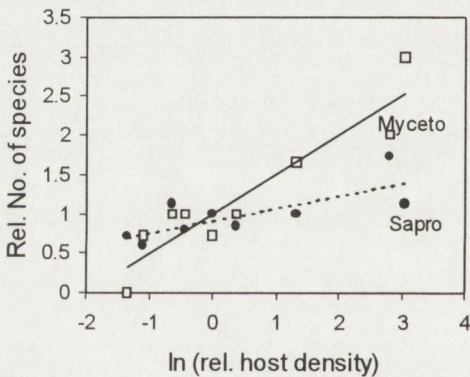


Fig. 5. Numbers of species of parasitoids of mycetophagous and saprophagous Diptera on plots of manipulated amount of leaf litter with different numbers of host densities. To eliminate the influence of yearly species and density turnover species number and densities were divided through the numbers on control plots of the same year (relative species density). Data from Hövemeyer (1992b) and Ulrich (1999c). Parasitoids of mycetophages: Variance explanation R^2 of the regression = 0.86, $P < 0.01$; parasitoids of saprophages: $R^2 = 0.58$, $P < 0.05$.

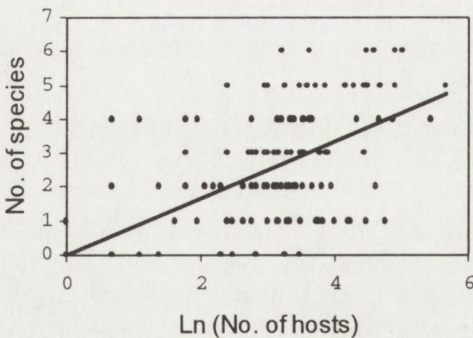


Fig 6. Number of parasitoid species (total of ten species) bred out of four dipteran host species from 147 dead *Arion ater* snails. Variance explanation R^2 of the regression = 0.23, $P < 0.01$.

4. DISCUSSION

The results of the present study are largely negative. Neither the predicted negative relationship between weight ratios and body weight, nor the left skewed species-weight distribution and a preponderance of maximum biomass accumulation in upper weight classes, nor the predicted right skewed species-productivity distributions were found. This raises the questions whether the basic assumptions of the theory were met.

First of all, the theory requires guilds with sufficiently common resources. This includes space, food and other resources. In our case the crucial factor is food. Ritchie and Olff (1999) argued that their theory should apply to trophic guilds like carnivores, granivores, herbivores and others. In this respect parasitoid host type guilds (which members are mostly at least oligophagous) and dipteran trophic guilds met the prerequisite. The mammalian herbivore and plant guilds studied by Ritchie and Olff are surely not more

similar in resource use than the parasitoid and dipteran guilds of this study.

More crucial to the theory is the other basic assumption: the fractal nature of resource distribution together with the concept of self similarity. Arguments based on fractal geometry have often inspired ecologists since Morse *et al.* (1985) showed that the surface of woody plants can be described by fractal geometry with a mean fractal dimension of about 1.44 (for recent reviews see Sugihara and May 1990, Gazda 1996, Kenkel and Walker 1997). Fractal based derivations are also appealing because of their elegance and simplicity.

Recent attempts to deduce basic ecological rules from concepts of self similarity include Harte *et al.*'s (1999) deduction of power function species-area curves, Kunin's (1998) fundamental diversity index, With and King's (1999) calculations of extinction thresholds, Sole *et al.*'s (1997) recognition of species extinction patterns in the fossil record, and especially West *et al.*'s (1997, 1999) derivations of allometric scaling laws of organisms. However, as Harte *et al.* (1999) self admit their theory does not explain species-area curves with slope values above 1 which had been reported by Strong (1974) and Rosenzweig and Sandlin (1997). Additionally, at small scales or coarser grain (larger units of area) species-area relationships are often better described by other models, especially exponential (Palmer and White 1994, Ulrich 2000).

The fractality of ecologically relevant surfaces has been shown several times (e. g. Morse *et al.* 1985, Shorrocks *et al.* 1991, Hatcher 1997, Kampichler 1999). Additionally, Morse *et al.* (1985) and Shorrocks *et al.* (1991) showed that fractal arguments can indeed be applied to distributions of arthropod body lengths, however, Stork and Blackburn (1993) found little agreement of their data from tropical rain forest guilds with a predicted fractal dimension of 1.44 (Morse *et al.* 1985).

If we admit that surfaces are indeed of fractal nature then theories based on self similarity should apply best for plants, herbivores or soil living organisms. These are guilds of the first or second trophic level. Guilds of higher trophic levels rely mainly on distributions of prey or hosts. These distributions may be governed by other factors. Indeed, With *et al.* (1997) showed in model

landscapes that the effect of fractal geometry was scale dependent and that at finer scales the relative abundance of habitats was even in a fractal landscape of greatest influence. Therefore, at finer scales, like the ones of this study, the relative abundance of food patches seems to be of more importance than fractal geometry. At larger scales the theory predictions may hold for species depending on surfaces. Whether they also hold for higher trophic levels seems at least unclear. This distinction may explain why Ritchie and Olff (1999) and Shorrocks *et al.* (1987) – using plants and herbivores – found good agreement with theory. It may also explain why this test and the test of Stork and Blackburn (1993) – using mainly higher trophic levels – failed.

ACKNOWLEDGMENTS I thank Prof. J. Buszko and Dr. Kartanas for critical and valuable suggestions on the manuscript. K. Hövemeyer kindly provided me with information on the dipteran communities. This work was in part supported by a grant from the Deutsche Forschungsgemeinschaft. The author received a scholarship from the Friedrich-Ebert-Foundation.

5. SUMMARY

This paper tests the recent published synthetic theory of biodiversity of Ritchie and Olff (1999) using data on parasitic Hymenoptera and soil living Diptera. Neither the predicted size dependent size ratio, nor the left skewed species number-size class ratios, nor right skewed species richness-productivity patterns were found (Figs 1, 2, 3, 4, 5 and 6, Tables 1, 2 and 3). It is concluded that the basic assumptions of the theory (self similarity of habitat, food, and resource distribution over ecological relevant scales) is not applicable at fine scales and to guilds of higher trophic levels. Whether in general the assumptions are applicable to plants and phytophages has to be decided by further studies.

6. REFERENCES

- Damuth J. 1981 – Population density and body size in mammals – *Nature*, 230: 699–700.
- Gazda A. 1996 – The fractal geometry and some of its application in ecology – *Wiadomości Ekologiczne*, 42: 163–178.
- Hatcher B. G. 1997 – Coral reef ecosystems: How much greater is the whole than the sum of the parts? – *Coral Reefs*, 16: S77 – S91.

- Hövmeyer K. 1985 – Die Zweiflügler (Diptera) eines Kalkbuchenwaldes: Lebenszyklen, Raum-Zeit-Muster und Nahrungsbiologie – Thesis Göttingen.
- Hövmeyer K. 1992a – Die Dipterengemeinschaft eines Kalkbuchenwaldes: eine siebenjährige Untersuchung – Zool. Jb. Syst. 119: 225–260.
- Hövmeyer K. 1992b – Response of Diptera populations to experimentally modified leaf litter input in a beech forest on limestone – Pedobiologia, 36: 35–49.
- Kampichler C. 1999 – Fractal concepts in studies of soil fauna – Geoderma, 88: 283–300.
- Kenkel N. C., Walker D. J. 1997 – Fractals in the biological sciences – Coenoses, 11: 77–100.
- Kunin W. E. 1998 – Extrapolating species abundance across spatial scales – Science, 281: 1513–1515.
- Maurer B. A., Brown J. H. 1988 – Distribution of energy use and biomass among species of North American terrestrial birds – Ecology, 69: 1923–1932.
- Morse D. R., Lawton J. H., Dodson M. M., Williamson M. H. 1985 – Fractal dimension of vegetation and the distribution of arthropod body lengths – Nature, 314: 731–733.
- Palmer M. W., White P. S. 1994 – Scale dependence and the species-area relationship – Am. Nat. 144: 717–740.
- Ritchie M. E., Olff H. 1999 – Spatial scaling laws yield a synthetic theory of biodiversity – Nature, 400: 557–560.
- Rosenzweig M. L., Sandlin E. A. 1997 – Species diversity and latitude: listening to area's signal – Oikos, 80: 172–176.
- Sole R. V., Manrubia S. C., Benton M., Bak P. 1997 – Self-similarity of extinction statistics in the fossil record – Nature, 388: 764–766.
- Sugihara G., May R. M. 1990 – Applications of fractals in ecology – Trends Ecol. Evol. 5: 79–86.
- Stork N. E., Blackburn T. M. 1993 – Abundance, body size and biomass of arthropods in tropical forest – Oikos, 67: 483–489.
- Strayer D. 1986 – The size structure of a lacustrine zoobenthic community – Oecologia, 69: 513–515.
- Strong D. R. 1974 – Nonasymptotic species richness models and the insects of British trees – Proc. Nat. Acad. Sci. USA 71: 2766–2769.
- Ulrich W. 1988 – Welche Faktoren beeinflussen die Populationen und die Strukturen der Gemeinschaften von bodenlebenden parasitoiden Hymenopteren in einem Kalkbuchenwald? – Thesis Göttingen.
- Ulrich W. 1998 – The parasitic Hymenoptera in a beech forest on limestone I: Species composition, species turnover, abundance and biomass – Pol. J. Ecol. 46: 261–289.
- Ulrich W. 1999a – The Hymenoptera of a dry meadow on limestone: Species composition, abundance and biomass – Pol. J. Ecol. 47: 29–47.
- Ulrich W. 1999b – The density-weight and the biomass-weight distribution can be generated by the species-weight distribution together with density fluctuations: evidence from model species distributions in the Hymenoptera. Pol. J. Ecol. 47: 87–101.
- Ulrich W. 1999c – Species composition, coexistence and mortality factors in a carrion exploiting community composed of necrophagous Diptera and their parasitoids – Pol. J. Ecol. 47: 49–72.
- Ulrich W. 1999d – Abundance, biomass and density boundaries in the Hymenoptera: analysis of the abundance-body size relationship and differences between forest and open landscape habitats – Pol. J. Ecol. 47: 73–86.
- Ulrich W. 2000 – On species-area relationships I: Fit of power function and exponential model – Pol. J. Ecol. 48: 3–20.
- West G. B., Brown J. H., Enquist B. J. 1997 – A general model for the origin of allometric scaling laws in biology – Science, 276: 122–126.
- West G. B., Brown J. H., Enquist B. J. 1999 – The fourth dimension of life: fractal geometry and allometric scaling of organisms – Science, 284: 1677–1679.
- With K. A., Gardner R. H., Turner M.G. 1997 – Landscape connectivity and population distributions in heterogeneous environments – Oikos, 78: 151–169.
- With K. A., King A. W. 1999 – Extinction thresholds for species in fractal landscapes – Conservation Biology, 13: 314–326.

(Received after revising April 2000)