

Species Abundance Distribution Patterns in Kashmir Himalayan Grasslands Along an Altitudinal Gradient

Zafar Reshi*, Anzar Ahmad Khuroo and B. A. Wafai

Department of Botany, University of Kashmir, Srinagar-190 006, J&K, India

*E-mail: zreshi@yahoo.com

ABSTRACT

Differences in the distribution of relative abundances between the species of plant communities have been remarkably little analysed and rarely have curves of different species abundance distribution models been fitted to field data. Thus, in the present study species abundance pattern of flowering plant assemblages in three grasslands along an elevational gradient were tested against twelve deterministic and stochastic models. Though the Valley-plain grassland shared only two species with sub-alpine grassland, yet the Zipf-Mandelbrot (zm) and stochastic Zipf-Mandelbrot (stoz) models correspond best with the observed species abundance patterns in the two grasslands. Such patterns reflect a successional process wherein the later colonists have more specific requirements and hence are rarer than the first species to arrive. Geometric series model provided a good explanation for patterns observed in the alpine grassland and the same is consistent with the occurrence of such a pattern in species poor communities exposed to harsh environmental conditions as are prevalent in alpine habitats.

Keywords: Relative abundance distribution, stochastic models, deterministic models, species-rank order

INTRODUCTION

The study of relative abundance patterns of species, which reflects the ability of species to survive and secure resources, has a long history in community ecology (Hubbell, 2001; Magurran, 2005). In such studies two approaches are

followed; one relates species' traits to their abundances along environmental gradients (Nash Suding et al., 2003) and the other is the modelling approach, inspired by the fact that the species abundance patterns (SADs) observed in a wide range of communities can be described by a few statistical models (Hubbell, 2001; Ulrich, 2001a). Because of the intriguingly simple geometric shapes of such rank-abundance curves (one axis of the curve representing species rank in a community and the other representing species abundance), a large number of different theoretical models have been put forth to explain the shape of SADs (Tokeshi, 1993; 1999; Hubbell, 2001; Magurran, 2004). These models can be classified into two main groups: deterministic distribution models and stochastic models based on assumed pattern of resource use. To the first group belong the models like, lognormal (Preston, 1962), the negative binomial (Pielou, 1977), the broken stick (MacArthur, 1957), the geometric series (Motomura, 1932), the log-series (Fisher et al., 1943), or the Zipf-Mandelbrot and fractal models (Frontier, 1985; Bell, 2000). The second group includes models

like, sequential breakage (Sugihara, 1980; Ulrich, 2001b), the niche apportionment (Tokeshi, 1990), the neutral (Hubbell, 2001), and the variability model (Ulrich, 2001c). Deterministic models assume that N individuals will be distributed amongst the S species in the assemblage in a predetermined way. Stochastic models, on the other hand, recognize that replicate communities structured according to the same set of rules will inevitably vary somewhat in terms of the relative abundances of species found there. Some of these models are more successful than others at describing species abundance distributions, but none are universally applicable to all ecological assemblages. This is because both species richness, and the degree of inequality in species abundances vary amongst assemblages (Magurran, 2004). In spite of this constraint, SADs have the power to shed light on the processes that determine the biological diversity of an assemblage. In fact, Tokeshi (1993) strongly advocated their use in community characterization and argued that species abundance patterns deserve equal and possibly even more attention than biodiversity. However, SADs have been mainly studied from a within habitat perspective (Tokeshi, 1999; Magurran, 2004) and variation in SADs in different but related communities have been rarely undertaken (Johansson et al., 2006). Thus, the present study aims to compute relative abundance patterns of the species in the three grasslands occurring at different altitudes and fit the stochastic and deterministic models to the observed data so as to find out the appropriate model that best fits the observed species abundance pattern and reflect on the factors that have a bearing on the community organization.

MATERIAL AND METHODS

Study Sites

Present study was carried out in Dachigam National Park (34° 5' to 34° 3' north latitude, and 74° 4' to 74° 5' east longitude) which represents the last abode of threatened Kashmir Stag (*Cervus elaphus hanglu*). The park is located in the state of Jammu and Kashmir at a distance of 21 km from the Srinagar city. It is roughly rectangular in shape with an area of 141 sq km. It is approximately 24 km in length and 6 km in breadth with altitude ranging from 1,600 meters to 4,400 meters above mean sea level (amsl). A sizeable portion of the National Park sustains grasslands and meadows which are used by the Kashmir stag as feeding grounds. The staff of the National Park burns these grasslands irregularly during the autumn season. For the present study the three selected grasslands represent a elevational gradient with Valley-plain grassland lying at an altitude of 1600 metres amsl, the sub-alpine grassland at 2700 metres amsl and the alpine grassland at an altitude of 3200 metres amsl.

Methods

The three selected grasslands were surveyed during the summer (June-August) of 2004. In each grassland 30 quadrats of 0.5 m² were randomly laid and abundance of the species per quadrat (0.5 m²) was calculated after Curtis and Cottam (1956). In case of the species with runner habit each node was taken equivalent to an individual and in respect of other rhizomatous species each upright shoot was considered as an individual (Singh, 1969).

In order to describe species abundance patterns of flowering plant assemblages of the grasslands, twelve types of models, briefly described in the Table 1, were fitted to the observed data. For assessing the goodness of fit we used the 95% confidence limit method (Tokeshi, 1990; Ulrich and Zalewski, 2006) and counted, for abundance-rank order plots, the number of data points that ranged outside the 95% confidence limits ($FR < conf$). In addition, sum of all squared log-residuals r_{test} of model expectation

and observed values was also used to find out the best fit model.

$$r_{test} = \sum_{i=1}^S (\text{obs} - \text{exp})^2$$

with obs and exp being the log transformed observed and expected abundances and S the number of species. The smaller r_{test} is, the better does a given model fit to a given dominance rank order distribution (Ulrich and Ollik, 2005).

Table 1. Description of the models used in the present study

S. No.	Model	Source	Basic features
Deterministic Models			
1.	Geometric series (geo)	Motomura (1932)	It is predicted to occur when species arrive at an unsaturated habitat at regular intervals of time, and occupy fractions of remaining niche space. It is assumed that the abundances of species are proportional to the amount of resource they utilize.
2.	Log-series (lser)	Fisher et al. (1943)	In contrast to geometric series, it results when the intervals between the arrival of the species are random rather than regular. It produces a slightly more even distribution of species abundance

Table 1 Contd.

3.	Lognormal (norm)	Preston (1948)	In this model the variable is the number of individuals per species (standardized by log transformation) and the determining factors are all the processes that govern community ecology. The majority of large assemblages studied by ecologists appear to follow a log normal pattern of species abundance. The near ubiquity of the log normal distribution pattern has been attributed, by some, to the mathematical properties of large data sets while others have advocated stronger biological underpinnings.
4.	Broken stick (bro)	MacArthur (1957)	This model equates the sub-division of niche space within a community to a stick broken randomly and simultaneously into S pieces. If each piece is thought of as the resource used by one species, the model postulates S species dividing the environment into S non-overlapping niches of randomly allocated size.
5.	Zipf-Mandelbrot (zm)	Zipf (1949)	It has been interpreted as reflecting a successional process in which later colonists have more specific requirements and hence are rarer than the first species to arrive. The model postulates a rigid sequence of colonists, with the same species always present at the same point in the succession in similar habitats.

Stochastic models

Table I Contd.

1.	Particulate niche (par)	MacArthur (1957)	The abundance-determining factor is accumulated as independent discrete units by the various species. That is, the species can be compared with urns into which particles (units of abundance) are tossed on independent random throws, each urn having equal probability. This hypothesis states that when the number of tosses becomes infinite, all species become equally abundant, since the number of individuals is bounded.
2.	Overlapping niche (over)	Tokeshi (1990)	Like broken stick model, here also environment is again compared with a stick, but each species is now independent of the others. In other words, the abundance of any species is determined by the distance between a pair of points thrown at random onto the stick
3.	Random fraction (ranf)	Tokeshi (1990)	It is a sequential breakage model in which the available niche space is initially divided, at random, into two pieces. One of these pieces is then selected at random for the second division and this process continues until all species are accommodated. The model represents a situation in which a new colonist competes for the niche of a species already in the community, and takes over a random proportion of this previously existing niche.
4.	Random assortment (rane, rapo)	Tokeshi (1990)	It is applicable to communities that are in a state of flux, perhaps because of major environmental changes and competition is not setting limits on species abundances. In such communities the abundances of species vary independently of one another.

Table I Contd.

Table 1 Contd.

5.	Dominance decay (ddec)	Tokeshi (1990)	It envisages a more uniform pattern of species abundance. In it the largest niche is invariably split. The size of the resulting fragments are chosen at random, and therefore, this model is a mirror image of the dominance pre-emption model.
6.	Power fraction (pow)	Tokeshi (1990)	Unlike majority of niche apportionment models, Power fraction model is applicable to species-rich assemblages. It envisages that niche space is initially subdivided at random. One of resulting niches is then selected and again split at random. The process continues until all species have been accounted for. The probability that a niche will be split is positively, though rather weakly, related to its size (x) through a power function K (that is x^K where K ranges from 0 to 1).
7.	Stochastic Zipf-Mandelbrot (stoz)	Ulrich (2001 a)	It is a stochastic equivalent of Zipf-Mandelbrot deterministic model.

* Model abbreviations are given in parentheses

RESULTS AND DISCUSSION

Floristic Composition

Species composition and their abundance in the three investigated grasslands is given in Table 2. Highest number of 26 species was recorded in the Valley-plain grassland with

dominance of *Bromus japonicus*, *Bothriochloa ischaemum*, *Cynodon dactylon* and *Poa pratensis* while *Themeda anathera* was the most dominant species among the 22 species inhabiting the sub-alpine grassland. Least number (17) of species was recorded in the alpine grassland with dominance of *Cynodon dactylon*.

Table 2. Species composition and their abundance in the three grasslands.

Valley plain	Abundance	Sub-alpine	Abundance	Alpine	Abundance
<i>Bromus japonicus</i>	67.69	<i>Themeda anathera</i>	106.1	<i>Cynodon dactylon</i>	34.04
<i>Bothriochloa ischaemum</i>	61.58	<i>Arthraxon prionoids</i>	8.43	<i>Myosotis caespitosa</i>	18.13
<i>Cynodon dactylon</i>	56.4	<i>Androsace rotundifolia</i>	6.5	<i>Potentilla argyrophylla</i>	15.13
<i>Poa pratensis</i>	46.19	<i>Silene vulgaris</i>	5.7	<i>Trifolium repens</i>	12.13
<i>Convolvulus arvensis</i>	19.32	<i>Medicago polymorpha</i>	4.79	<i>Poa pratensis</i>	11.5
<i>Arenaria serpyllifolia</i>	15.73	<i>Stachys seriaca</i>	3.76	<i>Iris ensata</i>	9.95
<i>Plantago lanceolata</i>	13.81	<i>Clinopodium vulgare</i>	3.55	<i>Trifolium pratense</i>	9.35
<i>Oxalis corniculata</i>	12.77	<i>Nepeta laevigata</i>	3.33	<i>Thymus serpyllum</i>	5.6
<i>Scandix pectiniferis</i>	10.47	<i>Lespedeza elegans</i>	3.29	<i>Hackelia uncinata</i>	5.12
<i>Vernonica persica</i>	9.68	<i>Solidago vifgaurea</i>	3	<i>Duchesnea indica</i>	4.85
<i>Lespedeza cuneata</i>	9.18	<i>Daucus carota</i>	2.5	<i>Arenaria griffithii</i>	4.69
<i>Crepis sancta</i>	7.61	<i>Artemesia absinthium</i>	2.45	<i>Galium aparine</i>	3.75
<i>Lotus corniculatus</i>	6.27	<i>Crepis kashmirica</i>	2.21	<i>Bistorta amplexicaule</i>	3.19
<i>Trifolium pratense</i>	5.95	<i>Indigofera heterantha</i>	2.2	<i>Polygonum affine</i>	2.84
<i>Vicia sativa</i>	5.17	<i>Euphorbia wallichii</i>	2	<i>Artemesia annua</i>	2.55
<i>Euphorbia helioscopia</i>	5.08	<i>Prunella vulgaris</i>	1.92	<i>Achillea millefolium</i>	2.15
<i>Medicago polymorpha</i>	4.32	<i>Lespedeza cuneata</i>	1.61	<i>Geranium pratense</i>	1.85
<i>Erodium cicutarium</i>	3.86	<i>Sium latijugum</i>	1.5		
<i>Capsella bursapastoris</i>	3.8	<i>Carpesium cernuum</i>	1.45		
<i>Ranunculus arvensis</i>	3.45	<i>Hypericum perforatum</i>	1.44		
<i>Poa bulbosa</i>	2.89	<i>Artemesia scoparia</i>	1.33		
<i>Poa annua</i>	2.8	<i>Myriactus wallichii</i>	1.29		
<i>Lithospermum arvense</i>	2.64				
<i>Sisymbrium loestlii</i>	2.43				
<i>Taraxacum officinalis</i>	2.07				
<i>Tragopogon kashmirianus</i>	1.6				

While the Valley-plain grassland shared two and three species with sub-alpine and alpine grasslands, respectively, the sub-alpine grassland did not share any species with the alpine grassland. Differences in the species richness and composition observed in the three grasslands might be a response to the elevation which provides a complex gradient where ecological factors vary in different spatial scales, and plants respond to different combinations of ecological factors (Barrera *et al.*, 2000; Colwell and Lees,

2000; Wang *et al.*, 2003; Carpenter, 2005).

Rank-abundance Pattern

Rankabundance plots of the three grasslands are presented in Figs. 1-3. Data (Table 3) show that Zipf-Mandelbrot (zm) and stochastic Zipf-Mandelbrot (stoz) models best fit the observed abundance pattern of the species in the Valley-plain and sub-alpine grassland, respectively.

It has been interpreted as reflecting a successional process in which later colonists have more specific requirements and hence are rarer than the first species to arrive (Frontier, 1985). For example, pioneer species have low cost, requiring few prior conditions while as the late successional species have a high cost, viz. the energy, time, and organization of the ecosystem *required before they can invade. On this basis* they will be rare and these differences between species give a Zipf or Zipf-Mandelbrot distribution (Wilson, 1991). Unlike General Lognormal model, in the Zipf-Mandelbrot model many factors are postulated to act sequentially

(Wilson, 1991). Though Tokeshi (1993) considers this model as no more biological than the log normal or log series, yet the model has been successfully applied in a number of studies (Reichelt and Bradbury, 1984; Barange and Campos, 1991), and continues to have application in both terrestrial (Wilson et al., 1996; Mouillot and Lepetre, 2000) and aquatic (Juhos and Voros, 1998) systems. *In respect of the alpine* grassland, geometric series (geo) model proved the best fit model for the species abundance pattern (Table 3). Many other studies have also reported occurrence of such a pattern of species abundance in species-poor communities exposed

Table 3. r_{test} values and 95% confidence limit test of the log-abundance-species-rank-order plots of the models tested.

Model*	r_{test}			FR < conf.		
	Valley plain grassland	Sub-alpine grassland	Alpine grassland	Valley plain grassland	Sub-alpine grassland	Alpine grassland
pow	153.34	324.64	165.21	0.038	0.045	0.059
ranf	618.42	313.38	472.36	0.385	0.364	0.176
rapo	41.99	205.41	16.896	0.731	0.409	1.000
rane	28.70	184.21	24.42	0.923	0.591	1.000
over	506.68	144.46	161.75	0.000	0.364	0.000
ddec	104.87	102.54	15.22	0.000	0.000	0.000
par	142.78	51.75	51.28	0.308	1.000	0.588
zm	15.76	14.87	31.21	0.962	1.000	0.941
stoz	196.54	13.32	81.46	0.039	1.000	0.000
bro	66.66	111.91	33.41	0.962	0.909	0.941
norm	36.71	57.74	132.15	0.923	0.818	0.000
lser	19156.37	339.73	241.08	0.269	0.000	0.235
geo	33.31	107.42	14.75	1.000	0.955	1.000

to harsh environmental conditions (Magurran, 2004); conditions common to alpine communities, including the alpine grassland studied during the present investigation.

Present study allows to refute the commonly held view of near ubiquity and pervasiveness of the Log normal distribution in communities (Gray, 1987). Also the observation that the Zipf-Mandelbrot rarely fits over the

whole range of abundances in a community is not supported by the current investigation. Moreover, the study brings out that altitude, through its effect particularly on the temperature-precipitation gradient, influences not only the species richness and composition of the grasslands but also has significant effect on SADs.

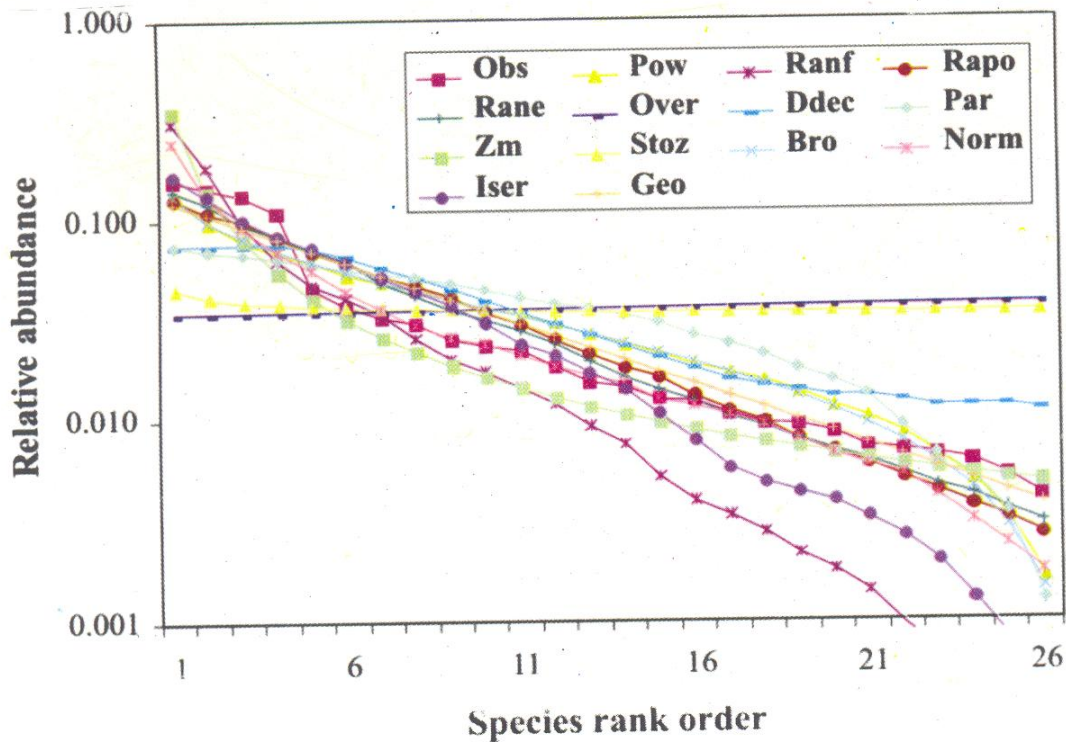


Fig. 1. Rank-order-log-abundance plots of the Valley-plain grassland fitted according to different models.

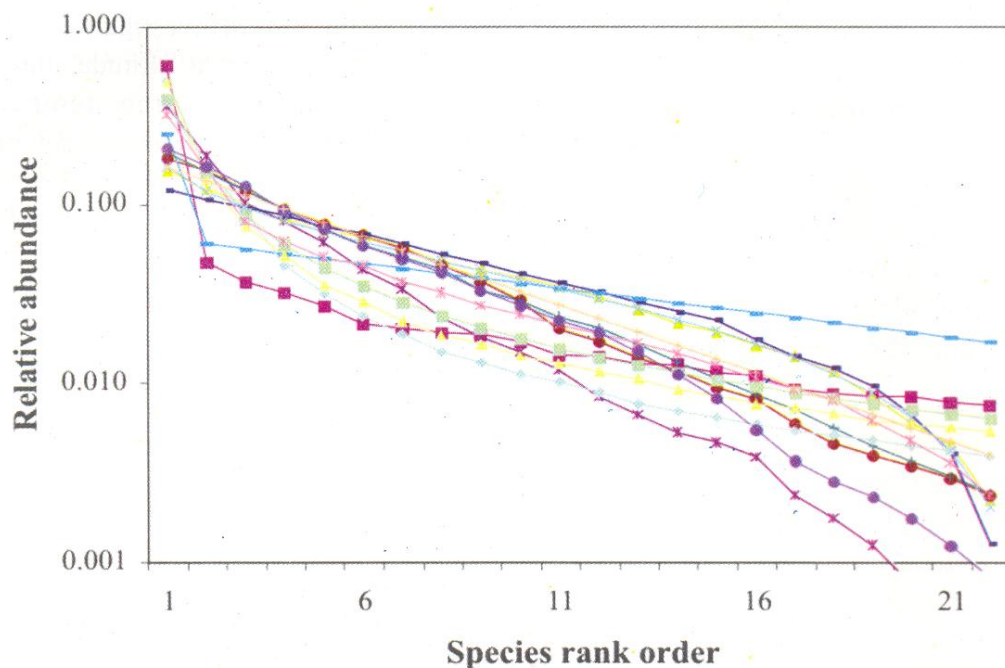


Fig. 2. Rank-order-log-abundance plots of the sub-alpine grassland fitted according to different models. (See Fig. 1 for legend).

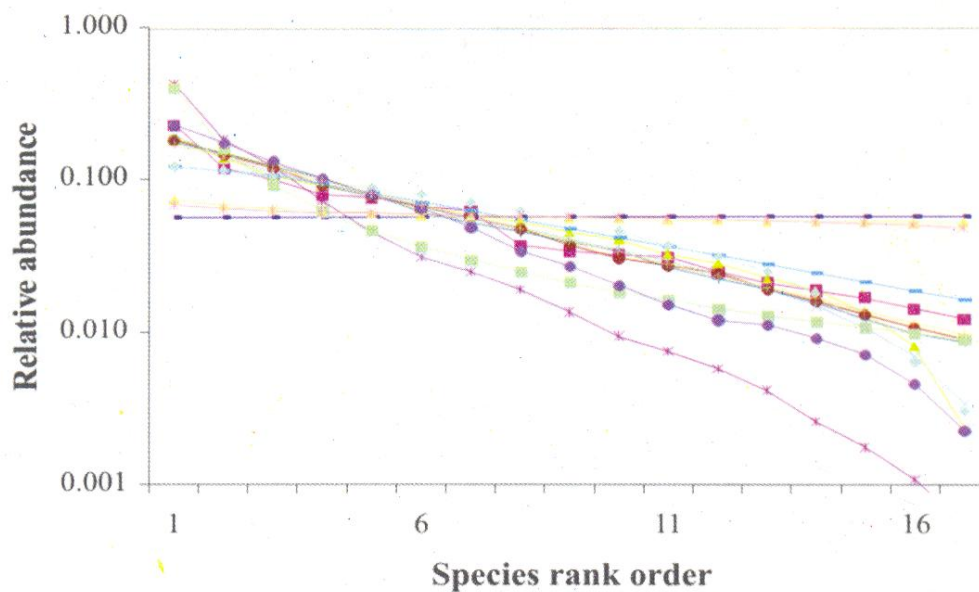


Fig. 3. Rank-order-log-abundance plots of the alpine grassland fitted according to different models. (See Fig. 1 for legend).

ACKNOWLEDGEMENTS

Authors are thankful to GB Pant Institute of Himalayan Environment and Development, Almora for financial assistance.

REFERENCES

- Barange, M. and Campos, B. 1991. Models of species abundance a critique and an alternative to the dynamics model. *Mar. Ecol. Prog. Ser.* **69**: 293-298.
- Barrera, M.D., Frangi, J.L., Richter, L.L., Perdomo, M.H. and Pinedo, L.B. 2000. Structural and functional changes in *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego, Argentina. *Journal of Vegetation Science* **11**: 179-188.
- Bell, G. 2000. The distribution of abundance in neutral communities. *American Naturalist* **155**: 606-617.
- Carpenter, C. 2005. The environmental control of plant species density on a Himalayan elevation gradient. *Journal of Biogeography* **32**: 999-1018.
- Colwell, R.K. and Lees, D.C. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution* **15**: 70-76.
- Curtis, J.T. and Cottam, G. 1956. *Plant Ecology Workbook (Laboratory, Field and Reference Manual)*. Burgers Publishing Company, Minnesota, USA.
- Fisher, R.A., Corbet, A.S. and Williams, C.B. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology* **12**: 42-58.
- Frontier, S. 1985. Diversity and structure in aquatic ecosystems. p. 253-312. In: *Oceanography and Marine Biology, An Annual Review* (M. Barnes, ed.), Aberdeen University Press, UK.
- Gray, J.S. 1987. Species-abundance patterns. p. 53-67. In: *Organization of Communities, Past and Present* (J.H.R. Gee and P.S. Giller, eds.), Blackwell Science, Oxford, UK.
- Hubbell, S.P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Johansson, F., Ebglund, G., Brodin, T and Gardfjell, H. 2006. Species abundance models and patterns in dragonfly communities: effect of fish predators. *Oikos* (in press)
- Juhos, S. and Voros, L. 1998. Structural changes during eutrophication of Lake Balaton, Hungary, as revealed by the Zipf-Mandelbrot model. *Hydrobiologia* **370**: 237-242.
- MacArthur, R.H. 1957. On the relative abundance of bird species. *Proc. Natl. Acad. Sci. USA* **43**: 293-295.
- Magurran, A.E. 2004. *Measuring Biological Diversity*. Blackwell Publishing Company, USA.

- Magurran, A.E. 2005. Species abundance distributions: patterns or process? *Functional Ecology* **19**: 177-181.
- Motomura, I. 1932. On the statistical treatment of communities. *Zoological Magazine Tokyo* **44**: 379-383.
- Mouillot, D. and Lepetre, A. 2000. Introduction of relative abundance distribution (RAD) indices, estimated from the rank frequency diagrams (RFD), to assess changes in community diversity. *Environmental Monitoring and Assessment* **63**: 279-295.
- Nash Suding, K., Goldberg, D.E. and Hartman, K.M. 2003. Relationships among species traits: separating levels of response and identifying linkage to abundance. *Ecology* **84**: 1-16.
- Pielou, E.C. 1977. *Mathematical Ecology*. John Wiley and Sons, New York.
- Preston, F.W. 1948. The commonness, and rarity, of species. *Ecology* **29**: 254-283.
- Preston, F.W. 1962. The canonical distribution of commonness and rarity. Part I and II. *Ecology* **43**: 185-215, 410-432.
- Reichelt, R.E. and Bradbury, R.H. 1984. Spatial patterns in coral reef benthos: multi-scale analysis of sites from three oceans. *Mar. Ecol. Prog. Ser.* **17**: 1-8.
- Singh, J.S. 1969. Influence of biotic disturbance on the preponderance and interspecific association of two common forbs in the grassland at Varanasi. *Tropical Ecology* **10**: 59-71.
- Sugihara, G. 1980. Minimal community structure: an explanation of species abundance patterns. *American Naturalist* **116**: 770-787.
- Tokeshi, M. 1990. Niche apportionment or random assortment: species abundance patterns revisited. *Journal of Animal Ecology* **59**: 1129-1146.
- Tokeshi, M. 1993. Species abundance patterns and community structure. *Advances in Ecological Research* **24**: 111-186.
- Tokeshi, M. 1999. *Species Coexistence*. Blackwell Publishing Company, USA.
- Ulrich, W. 2001a. Models of relative abundance distributions. I: model fitting by stochastic models. *Polish Journal of Ecology* **49**: 145-157.
- Ulrich, W. 2001b. Estimating species numbers by extrapolation: a cautionary note. *Polish Journal of Ecology* **49**: 299-305.
- Ulrich, W. 2001c. Relative abundance distributions of species: The need to have a new look at them. *Polish Journal of Ecology* **49**: 393-407.
- Ulrich, W. and Ollik, M. 2005. Limits to the estimation of species richness: The use of relative abundance distributions. *Diversity and Distributions* **11**: 265-273.
- Ulrich, W. and Zalewski, M. 2006. Abundance and co-occurrence patterns of core and satellite species of ground beetles on small lake islands. *Oikos* (in press).

- Wang, G.H., Zhou, G.S., Yang, L.M. and Li, Z.Q. 2003. Distribution, species diversity and life form spectra of plant communities along an altitudinal gradient in the northern slopes of Qilianshan Mountains, Gansu, China. *Plant Ecology* **165**: 169-181.
- Wilson, J.B. 1991. Methods of fitting dominance/diversity curves. *Journal of Vegetation Science* **2**: 35-46.
- Wilson, J.B., Wells, T.C.E., Trueman, I.C., Jones, G., Atkinson, M.D., Crawley, M.J., Dodd, M.E. and Silvertown, J. 1996. Are there assembly rules for plant species abundance? An investigation in relation to soil resources and successional trends. *Journal of Ecology* **84**: 527-538.
- Zipf, G.K. 1949. *Human behaviour and the principle of least effort*. Hafner, New York, USA.