

Different ways of constructing octaves and their consequences on the prevalence of the bimodal species abundance distribution

Jorge M. Lobo and Mario E. Favila

Lobo, J. M. and Favila, M. E. 1999. Different ways of constructing octaves and their consequences on the prevalence of the bimodal species abundance distribution. – *Oikos* 87: 321–326.

Several studies on dung beetle communities suggest that their species abundance distribution is bimodal. This bimodality has been explained as a consequence of the mixture of local and non-local species in the communities. In this paper we demonstrate that bimodal distribution in dung beetles is a consequence of the method of octave construction, which increases the number of species present in the first octave. Although we do not rule out the existence of bimodality in species abundance distributions, we suggest that this should be confirmed by large sampling programs done at local and regional levels, and by the correct application of the octave construction method.

J. M. Lobo, Dept Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), c/ José Gutiérrez Abascal, 2, E-28006 Madrid, Spain (mcnj117@mmcn.csic.es). – M. E. Favila, Dept Ecología y Comportamiento Animal, Instituto de Ecología, Apartado Postal 63, 91000 Xalapa, Veracruz, Mexico.

The lognormal distribution model is one of the most commonly used for analysing the relationship between the number of species and their relative abundance in plant and animal communities, and it has been found to fit in a high variety of ecological data (Tokeshi 1993). In Preston's original formulation (Preston 1948, 1962), the frequencies of the observed number of species are grouped in abundance classes or octaves which have a logarithmic scale of base 2, so that successive octaves represent a doubling of the previous one. With this method of grouping, species abundance data take the form of a symmetrical normal curve truncated on the left (May 1975, Pielou 1975, Sugihara 1980). The interpretation of the underlying ecological processes that generate the lognormal truncated pattern is still confused (see May 1975, Sugihara 1980, Ugland and Gray 1982, Tokeshi 1990, 1993, 1996).

Several studies on local and regional communities of dung beetles (Hanski 1983 and 1991, Cambefort 1991, Hanski and Cambefort 1991, Hanski and Krikken 1991, Lumaret and Stienet 1991, Chown and

Steenkamp 1996) suggest that the log-transformed species abundance distribution is not unimodal, but, rather, bimodal. As far as we know, such bimodality has only been reported in dung beetle studies. Are dung beetle communities really bimodal?

For the correct construction of octaves it is necessary to consider some methodological requirements. In this paper we examine these requirements to, later, analyse if the bimodal species abundance distributions depend on the way in which the data are grouped in octaves. To do that, we reexamine the original data of all papers where bimodality has been found in dung beetle communities. Finally, we comment on some theoretical implications of the bimodal species abundance assumption.

Octave construction

Preston (1948, 1962) proposed a way in which the relative abundance of species can be grouped into inter-

Accepted 15 February 1999

Copyright © OIKOS 1999

ISSN 0030-1299

Printed in Ireland – all rights reserved

vals (octaves). Preston (1948) said, "An octave is simply an interval of two-to-one. On the piano it may be from C to C': similarly in our ecological studies, it is the interval 4-to-8 or 6-to-12". So, a species that falls on a group boundary, for example one represented by 4 individuals, contributes with half a species to the octave B (2-4) and half to C (4-8). The first octave or octave A (1-2) contains half the species represented by one individual (singletons) and half represented by two individuals (doubletons). Half the singletons are assigned to the octave < 1 or octave 0-to-1.

Preston represented graphically the value of species for octaves < 1 by an upward-pointing arrow, meaning that the true number for this range is above the tip of the arrow. The left boundary of the first octave (1-2) is the "veil line" which defines on the left those relatively uncommon species belonging to different octaves, whose theoretical representation is appreciably less than one specimen, and for this reason will be missing from the sample. The sample shows clearly what the universe is like to the right of the veil line, but we have to infer what it is like to the left. In this way, truncation of the curve on the left, at the veil line, is inevitable in most of the studies (Pielou 1977). As the sample size increases the veil line moves to the left, revealing the less abundant species (Preston 1948). However, some studies that use very exhaustive data suggest that the very well-sampled assemblages have a left-skewed distribution with more rare than common species (Nee et al. 1991, Gregory 1994).

There are three methodological considerations in the classes construction of the lognormal distribution. First, the choice of the scale for intervals (\log_2 , \log_3 or any other), because it affects the estimated parameters and the power of the goodness-of-fit test (Colwell and Coddington, 1995). Second, each class is required to contain a constant increase with respect to the previous class. Third, the divisions between the classes should be equally spaced on the logarithmic scale (Williams 1964).

The use of \log_2 (0 to 1, 1 to 2, 2 to 4, ...), is the conventional procedure proposed by Preston for the octaves construction, even though a \log_3 scale (1, 2 to 4, 5 to 13, ...) has the advantage of not requiring the splitting of the integer values (Williams 1964). The choice of the scale is arbitrary, but a large interval reduces the number of classes obtained. Both with \log_2 (method A) and \log_3 (method B), each interval is a geometric increase of the previous one, and the boundaries or dividing points among classes are equally spaced on the log scale (Fig. 1 A, B).

These three considerations have not always been taken into account. For example, in several papers and books (see Krebs 1989), the classes are 1, 2 to 3, 4 to 7, ... (method C), and each octave contains twice the number of integers as the previous one, but the boundaries (0.5, 1.5, 3.5, ...), are not equally spaced on a logarithmic scale ($-0.301, 0.176, 0.544, 0.875, \dots$)

(Williams 1964). Consequently, the greatest distance between two boundaries is found between the first and the second octave, with distances decreasing in successive octaves. This method slightly overvalues the contribution of the first octaves (see Fig. 1C).

The case of dung beetles

Checking the literature on local and regional dung beetle communities and their species abundance, we found that they have been studied with different grouping methods, all based on Preston's proposal of doubling the successive octaves. Hanski (1983) used the octaves 1 to 2, 2 to 4, 4 to 8, ... (method D), and all the species with one individual (singletons) were retained in the octave 1-2, adding to this half the species with two individuals (doubletons). This produced an apparent bimodal distribution with many rare species. However, when half of the species with 1 individual were omitted, the curve had a typical lognormal distribution (see Fig. 3 in Hanski 1983). In subsequent studies (Hanski 1991, Hanski and Cambefort 1991, Hanski and Krikken 1991) the classes were 1 to 2, 3 to 4, 5 to 8, ... (method E) resulting in a bimodal distribution, but clearly 3-4 is not a doubling. In Staphylinidae communities, bimodality has also been found (Hanski and Hammond 1986, Hanski 1989) using the method of octave construction of Hanski (1983). Thus, when we use the abundance classes of methods D and E (Fig. 1), the second octave does not contain double the integers of the first. These two erroneous methods of octave construction have been used on some other occasions (see, e.g., May 1981 and Magurran 1988), in spite of the fact that they increase the number of species in the first octave.

We could not understand the grouping method presented for two dung beetle localities (Barro Colorado, Hanski and Cambefort 1991; Alps, Lumaret and Stiernet 1991), so the bimodal distribution is unclear to us. Chown and Steenkamp (1996) also found bimodal distributions for species abundance data, though they did not give indications about the method used for the octaves construction.

With the method of fitting a truncated log normal distribution proposed by Pielou (1975) and the conventional procedure proposed by Preston for the octaves construction, we analysed all dung beetle data where species abundance was examined (Table 1). We use the Kolmogorov-Smirnov one-sample with Lilliefors corrected critical values (Legendre and Legendre 1983) to compare the expected and the observed patterns of species abundance distribution. This test is more powerful than the χ^2 test and it can be applied to very small samples (Siegel and Castellan 1988, Tokeshi 1993).

The dung beetle abundance data was not significantly different from the theoretical truncated lognormal distribution, except for the Oxford data. These last data did not differ from a uniform distribution ($D = 0.168$, $0.2 > p > 0.1$). So, although the lognormal distribution according to the erroneous methods of octaves construction suggests a bimodal distribution in some localities, the Preston method eliminates this trend towards bimodality in all cases (Fig. 2). The lognormal distribution also fits well the data from the Alps and Barro Colorado presented by Hanski and Cambefort (1991) as graphical evidence of bimodality.

Discussion

The papers on dung beetle communities here reviewed violated the assumptions for the octaves construction. The most important errors are that they did not incorporate the 0 to 1 octave and overestimated the 1 to 2

octave. In others words, the cited studies incorporated the unsampled part of the universe in the sampled part and did not consider the "veil line". This produced an apparent bimodal distribution in the species abundance relations due to the higher contribution of rare species.

The absence of lognormality in a heterogeneous community is an uncommon result (Williams 1964, Gaston 1994), and is more likely due to a loss than to an increase in rare species (Ugland and Gray 1982). The data based on dung beetle communities provide, as we know, the only examples of bimodal distributions in nature and have been used in several recent papers and books to analyse the abundance and distribution of species at local and regional levels (e.g. Gaston 1994, Brown 1995). Hanski and Cambefort (1991) considered that bimodal abundance distributions are uncommon in the literature on insects due to the difficulties of sampling their communities. In contrast, in dung beetle communities that can be easily and exhaustively sampled, the bimodality can be observed. The bimodal

species with 1 individual	16
species with 2 individuals	4
species with 3 individuals	4
species with 4 individuals	4

abundance class	A			B		C		D		E	
	0-1	1-2	2-4	1	2-4	1	2-3	1-2	2-4	1-2	3-4
number of species	8	10	8	16	12	16	8	18	8	20	8

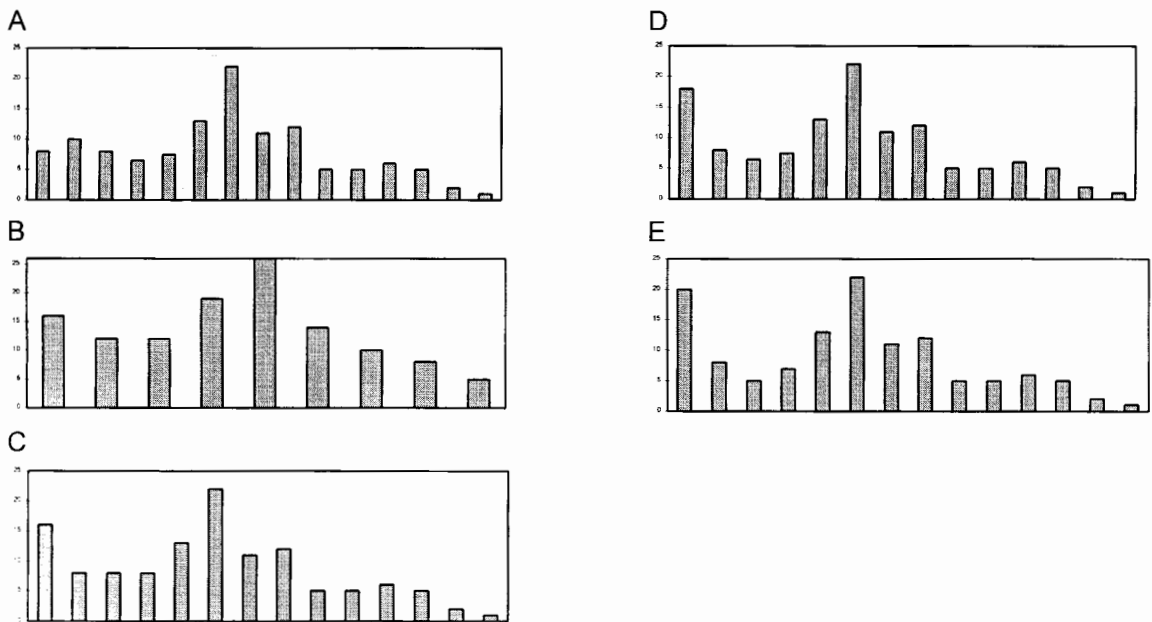


Fig. 1. Number of dung beetle species with 1 to 4 individuals; number of species in the two or three first octaves; and frequency histograms according to the five methods of octave construction mentioned in the text. A is the original Preston method with log₂; B is the log₂ method proposed by Williams (1964); C is a widely used method where the boundaries among classes are not equally spaced on a logarithmic scale (Williams 1964). Finally, D and E are erroneous methods in which the second octave does not contain double the integers of the first. Data from Aboukomakro, one African savanna locality used as evidence of bimodal distribution in dung beetle communities (Hanski and Cambefort 1991).

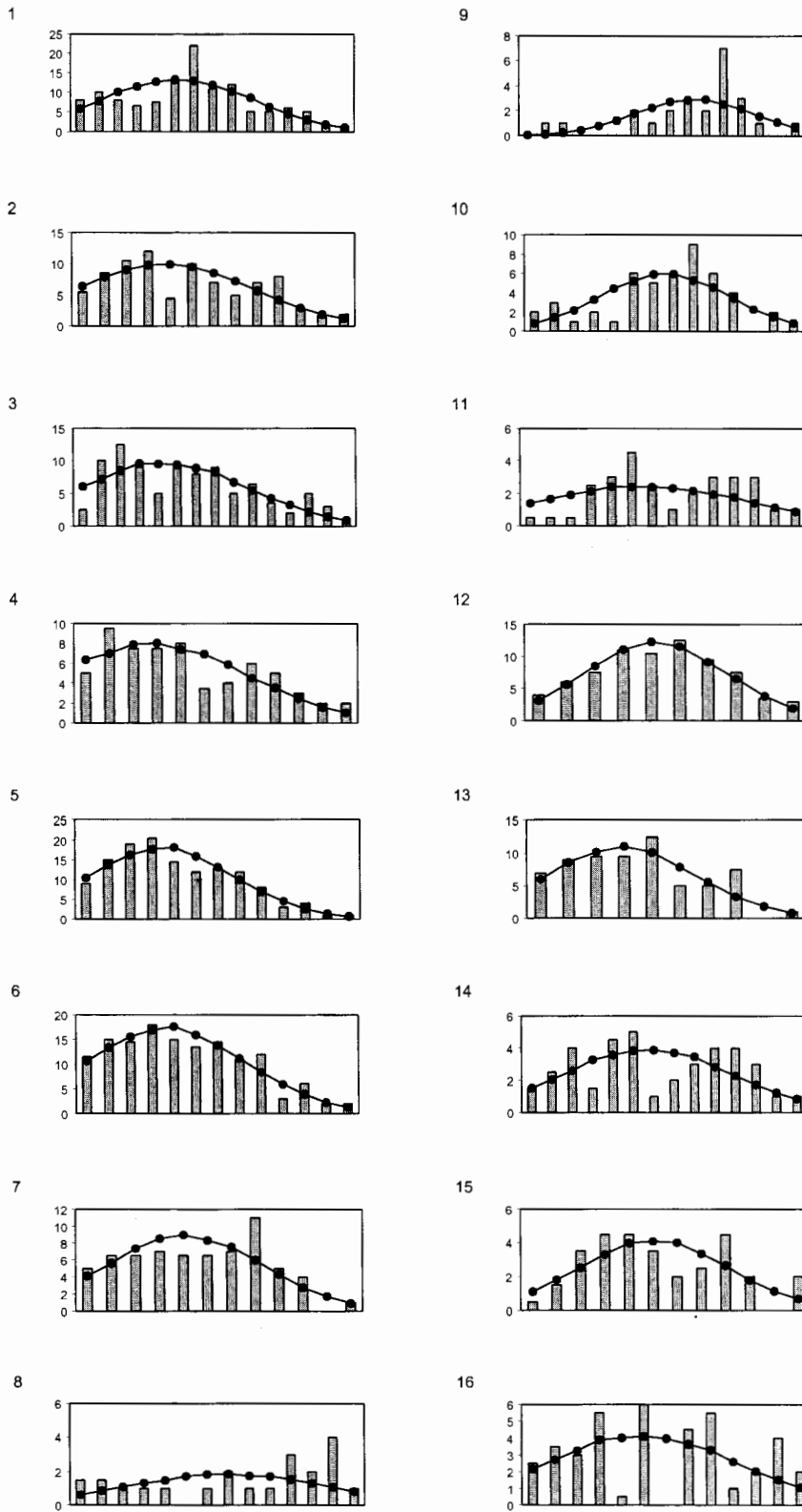


Fig. 2. Lognormal truncated species abundance distributions for the studies listed in Table 1 according to Preston's original method of octaves construction. The line is the adjusted truncated lognormal distribution.

Table 1. Data sources of all papers where bimodality has been found in dung beetle communities, their respective localities; and results of the Kolmogorov-Smirnov one-sample test with Lilliefors corrected critical values (Legendre and Legendre 1983), to compare the observed and the expected values of species abundance according to a truncated lognormal distribution (Pielou 1975), with the Preston method of octaves construction.

Reference	Localities	Lognormal truncated test
1 Cambefort (1991). Table B.9 (2)	Aboukoumekro	$D = 0.067,$ $0.2 > p > 0.1$
2 Cambefort (1991). Table B.9 (2)	Sipilou	$D = 0.067,$ $p > 0.3$
3 Cambefort (1991). Table B.9 (2)	Lamto	$D = 0.048,$ $p > 0.3$
4 Cambefort (1991). Table B.9 (2)	La Marahoué	$D = 0.075,$ $p > 0.3$
5 Cambefort (1991). Table B.9 (2)	Kapkin	$D = 0.038,$ $p > 0.3$
6 Cambefort (1991). Table B.9 (2)	Wango Fitini	$D = 0.020,$ $p > 0.3$
7 Hanski (1983)	Borneo	$D = 0.081,$ $0.3 > p < 0.2$
8 Hanski (1991). Table B.5	Oxford	$D = 0.226,$ $p = 0.01$
9 Lumaret and Stiernet (1991). Table 14.2	Alps	$D = 0.156,$ $p = 0.2$
10 Hanski and Cambefort (1991). Table B.12	Barro Colorado	$D = 0.077,$ $p > 0.3$
11 Hanski and Krikken (1991). Table B.10 (2)	Sulawesi	$D = 0.137,$ $p = 0.3$
12 Cambefort and Walter (1991). Table B.11 (1)	Tai forest	$D = 0.031,$ $p > 0.3$
13 Cambefort and Walter (1991). Table B.11 (2)	Makokou	$D = 0.039,$ $p > 0.3$
14 Chown and Steenkamp (1996)	South African savanna (year)	$D = 0.100,$ $p > 0.3$
15 Chown and Steenkamp (1996)	South African savanna (summer-92)	$D = 0.069,$ $p > 0.3$
16 Chown and Steenkamp (1996)	South African savanna (summer-93)	$D = 0.105,$ $p > 0.3$

species abundance distributions imply that the communities might be composed of a mixture of local and non-local species. In the latter group of species, there are some that occur thanks to the rescue effect, although they do not have stable, local breeding populations (Hanski et al. 1995a, b). So, if a minimum viable population size exists for local species, a second peak would appear in very large and exhaustive samples due to the vagrant species. We do not rule out this result appearing in nature but, at present, the graphic evidence to support it are unacceptable due to the way in which the species abundance has been grouped in octaves.

We suggest that to demonstrate bimodality in the species-abundance distribution it is necessary to con-

duct large sampling programmes at local scale. Also it would be convenient to use a single, homogeneous and consistent method of octaves construction; and to determine if the communities include rare, non-local species.

Acknowledgements – Thanks to Ilkka Hanski, Kevin J. Gaston and Adrian L. V. Davis for their comments and suggestions.

References

- Brown, J. H. 1995. *Macroecology*. – Univ. of Chicago Press, Chicago.
- Cambefort, Y. 1991. Dung beetles in tropical savannas. – In: Hanski, I. and Cambefort, Y. (eds), *Dung beetle ecology*. Princeton Univ. Press, Princeton, NJ, pp. 156–178.
- Cambefort, Y. and Walter, P. 1991. Dung beetles in tropical forest in Africa. – In: Hanski, I. and Cambefort, Y. (eds), *Dung beetle ecology*. Princeton Univ. Press, Princeton, NJ, pp. 198–229.
- Chown, S. L. and Steenkamp, H. E. 1996. Body size and abundance in a dung beetle assemblage: optimal mass and the role of transients. – *Afr. Entomol.* 4: 203–212.
- Colwell, R. K. and Coddington, J. A. 1995. Estimating terrestrial biodiversity through extrapolation. – In: Hawksworth, D. L. (ed.), *Biodiversity. Measurement and estimation*. Chapman and Hall, London, pp. 101–118.
- Gaston, K. J. 1994. *Rarity*. – Chapman and Hall, London.
- Gregory, R. D. 1994. Species abundance patterns of British birds. – *Proc. R. Soc. Lond. B* 257: 299–301.
- Hanski, I. 1983. Distributional ecology and abundance of dung and carrion-feeding beetles (Scarabaeidae) in tropical rain forest in Sarawak, Borneo. – *Acta Zool. Fenn.* 167: 1–45.
- Hanski, I. 1989. Dung beetles. – In: Lieth, H. and Wagner, J. A. (eds), *Ecosystems of the World, 14b Tropical forest*. Elsevier, Amsterdam, pp. 489–511.
- Hanski, I. 1991. North temperate dung beetles. – In: Hanski, I. and Cambefort, Y. (eds), *Dung beetle ecology*. Princeton Univ. Press, Princeton, NJ, pp. 75–96.
- Hanski, I. and Hammond, P.M. 1986. Assemblages of carrion and dung Staphylinidae in tropical rain forest in Sarawak, Borneo. – *Ann. Entomol. Fenn.* 52: 1–19.
- Hanski, I. and Cambefort, Y. 1991. Spatial processes. – In: Hanski, I. and Cambefort, Y. (eds), *Dung beetle ecology*. Princeton Univ. Press, Princeton, NJ, pp. 283–304.
- Hanski, I. and Krikken, J. 1991. Dung beetles in tropical forest in South-East Asia. – In: Hanski, I. and Cambefort, Y. (eds), *Dung beetle ecology*. Princeton Univ. Press, Princeton, NJ, pp. 179–197.
- Hanski, I., Pakkala, T., Kuussaari, M. and Lei, G. 1995a. Metapopulation persistence of an endangered butterfly in a fragmented landscape. – *Oikos* 72: 21–28.
- Hanski, I., Pöyri, J., Pakkala, T. and Kuussaari, M. 1995b. Multiple equilibria in metapopulations dynamics. – *Nature* 377: 618–621.
- Krebs, C. J. 1989. *Ecological methodology*. – Harper and Row, New York.
- Legendre, L. and Legendre, P. 1983. *Numerical ecology*. – Elsevier, Amsterdam.
- Lumaret, J. P. and Stiernet, N. 1991. Montane dung beetles. – In: Hanski, I. and Cambefort, Y. (eds), *Dung beetle ecology*. Princeton Univ. Press, Princeton, NJ, pp. 242–254.
- Magurran, A. E. 1988. *Ecological diversity and its measurement*. Princeton Univ. Press, Princeton, NJ.
- May, R. M. 1975. Patterns of species abundance and diversity. – In: Cody, M. L. and Diamond, J. M. (eds), *Ecology and evolution of communities*. Harvard Univ. Press, Cambridge, MA, pp. 81–120.

- May, R. M. 1981. Patterns in multi-species communities. – In: May, R.M (ed.), *Theoretical ecology: principles and applications*. Blackwell, Oxford, pp. 197–227.
- Nee, S., Harvey, P. H. and May, R. M. 1991. Lifting the veil line on abundance patterns. – *Proc. R. Soc. Lond. B* 243: 161–163.
- Pielou, E. C. 1975. *Ecological diversity*. – Wiley, New York.
- Pielou, E. C. 1977. *Mathematical ecology*. – Wiley, 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. – *Ecology* 43: 185–215, 410–432.
- Siegel, S. and Castellan, N. J. 1988. *Nonparametric statistics for the behavioural sciences*. McGraw-Hill, New York.
- Sugihara, G. 1980. Minimal community structure: an explanation of species abundance patterns. – *Am. Nat.* 116: 770–787.
- Tokeshi, M. 1990. Niche apportionment or random assortment: species abundance patterns revisited. – *J. Anim. Ecol.* 59: 1129–1146.
- Tokeshi, M. 1993. Species abundance patterns and community structure. – *Adv. Ecol. Res.* 24: 111–186.
- Tokeshi, M. 1996. Power fraction: a new explanation of relative abundance patterns in species-rich assemblages. – *Oikos* 75: 543–550.
- Ugland, K. I. and Gray, J. S. 1982. Lognormal distributions and the concept of community equilibrium. – *Oikos* 39: 171–178.
- Williams, 1964. *Patterns in the balance of nature and related problems in quantitative ecology*. – Academic Press, London.