CORRESPONDENCE

A typing error in Tokeshi's test of bimodality

One way to describe patterns of species distribution is to plot the frequency histograms using species–range-size data (Gaston, 1994; Brown, 1995; Gaston & Blackburn, 2000). Usually the untransformed geographical ranges of species are distributed following a 'hollow curve', i.e. most species have narrow ranges and very few have widespread distributions. This highly 'right-skewed' curve has been regarded as unimodal (e.g. Gaston, 1994). In some cases, however, the species–range-size distribution shows a bimodal pattern (Hanski, 1982; Brown, 1984, 1995; Gaston, 1994; Gaston & Blackburn, 2000), in which to the left-hand mode is added a right-hand mode generated by the widespread group of species that occur in almost all sampled sites. The 'core-satellite species hypothesis' (Hanski, 1982) and the 'resource usage model' (Brown, 1984, 1995) were proposed to explain the finding that a few species are regionally common (widespread) and locally abundant (the 'core' species in Hanski's model; the generalists or broad-niched species in Brown's model), while most species can be regarded as having smaller ranges and low local abundances (the 'satellite' species in Hanski's model; the specialists or narrow-niched species in Brown's model).

Alternatively, bimodality may occur only as a sampling artefact (Gaston, 1994). Rare species are, by definition, difficult to sample and sensitive to the sampling method used (Gaston, 1996); consequently, the left-hand mode is overestimated. Moreover, if the sites are highly homogeneous throughout all the measured range, the right-hand mode may be overestimated by the inclusion of widespread habitat specialist species (Gaston, 1994; see also Gaston & Blackburn, 2000). Bimodality may also simply be a consequence of a small number of sites being studied, so that some species occupy all of them (e.g. Williams, 1964).

Most early discussions of range-size distribution did not test formally for bimodality, perhaps because no simple test was available. This gap was filled by Tokeshi (1992), who proposed a statistical test for bimodality that permits the calculation of the probability of obtaining an observed frequency value in the two observed extreme classes (left and right) under the null hypothesis of random occurrence of species in a region. Coincident with the growing interest in macroecology (see Gaston, 1994; Brown, 1995; Maurer, 1999; Gaston & Blackburn, 2000), the availability of this type of

statistical test greatly improves the description and interpretation of frequency distribution patterns.

Collins & Glenn (1997), among others, applied Tokeshi's statistical test to test for bimodality in range-size distributions for grasshoppers, small mammals, plants and birds, but introduced a typing error in the formula used to calculate the probability of the left- and right-most classes. Although such errors may occur easily during manuscript preparation, final printing, or other associated processes, as we will show below, this particular error has had some consequences in recent applications of the model.

The test for one-sided skewness of species–range-size distributions is developed by defining, as the null hypothesis, that the distribution of species over all the size bins is uniform or random. Under this hypothesis and also assuming that the sampling is random, the probability of one given species falling in one given size bin is $h = 1/n_c$, where n_c is the number of size bins. The probability (P) of occurrence of a given absolute frequency f or higher is given by the upper-probability of a binomial distribution:

$$P(F > f) = \sum_{i=f}^{N} \frac{N!}{i!(N-i)!} h^i (1-h)^{N-i}$$

where F is a random variable that describes the event of a species occurring in a given size bin with probability h of success, and N is the total number of sampled species. The null hypothesis is rejected if the probability is smaller than a defined significance level (normally 0.05 or 0.1).

We found a typing error in Collins & Glenn (1997), in which '$(1-h)^{N-i}$' was replaced by '$(1-h)^{N-1}$'. Unfortunately, at least three recent studies (Guo *et al.*, 2000; Van Rensburg *et al.*, 2000; Perelman *et al.*, 2001) have referred to the incorrect equation in Collins & Glenn (1997). Applying the correct equation to the data of Van Rensburg *et al.* (2000) implies that half the datasets considered as bimodal are actually unimodal with a non-significant right mode. Also, reanalysing the data of Guo *et al.* (2000) shows that while the general patterns (i.e. bimodality vs. unimodality) remain the same, most P-values are now larger than those originally reported, in the case of unimodal distributions rendering the mode less significant following Tokeshi's (1992) diagnosis in Table 1 (p. 260). Moreover, we believe somewhat different results would be produced if the correct model were used in Collins & Glenn (1997), unless the typing error was simply a printing error (i.e. all the calculations actually used the correct equation). In Perelman *et al.* (2001) the datasets are clearly unimodal, but another typing error is evident in the text where P_l and P_r should be interchanged in p. 568, because the value

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range of between 10^{-11} and 10^{-15} should apply to P_l and not to P_r.

The best way to avoid this type of error is always to consult the original references and to compare with others that have used such original materials. A recent book on macroecology (Gaston & Blackburn, 2000) presents the correct equation (p. 102). Hopefully our short note will help avoid further use of the incorrect version of the equation.

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