Species diversity

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Volume 4, pp 2086–2092

in

Encyclopedia of Environmetrics
(ISBN 0471 899976)

Edited by

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Species diversity

Species diversity, the taxonomic variety of living organisms, is one of the three principal levels of biological diversity which include genetic diversity within species, species diversity and **ecosystem** or community (*see* **Community, ecological**) diversity [8]. In much environmental assessment, however, **biodiversity** is identified as synonymous with species diversity and measured by the number of species in an area – the **species richness**.

While the species is often seen as the fundamental unit in ecology, using the number of species to measure diversity requires the resolution of a number of issues [5]. First, there is the choice of taxonomic group, since differences in the species concept and the levels of discrimination applied in different taxa mean that species counts cannot automatically be combined across groups. Measuring species richness at the global or large regional scale often runs into problems of synonymy, the same species being given different names in different regions [28]. A simple species count also gives all species equal value, which may be inappropriate from a conservation standpoint. Furthermore, with more mobile taxa such as birds, the total count can be substantially inflated by transient vagrants that may be better omitted from environmental comparisons. These issues will vary in importance, and their resolution will depend on the objective of the diversity assessment. An even more pervasive problem arises in the estimation of species richness from samples.

Assessing Species Richness from Samples

A complete census of species in an area is rarely feasible, except for highly visible and closely studied taxa such as birds and plants. Assessment is therefore usually based on samples from the population, but the species count then depends on sampling effort.

Plotting species count against sampling effort produces a species accumulation curve with decreasing slope, as shown in Figure 1. Sampling effort may be defined by the number of samples, the time or area sampled, or the number of individuals examined. If the samples represent a small and random proportion of individuals from the study population, the total species count S_T may be equated with the asymptote of the species accumulation curve. This curve

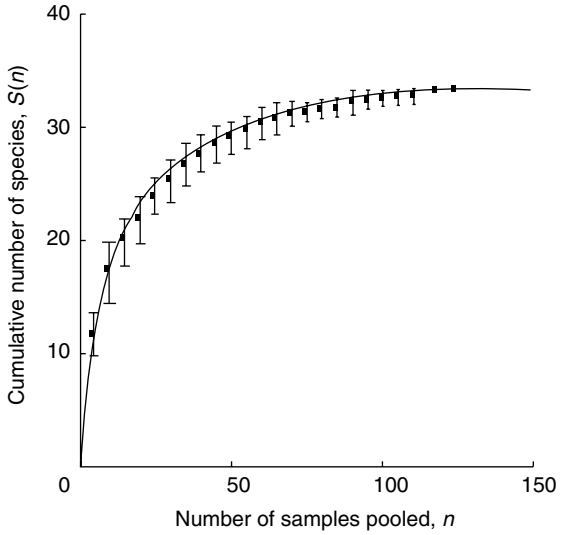

Figure 1 Species accumulation curve for seedlings germinating from 121 soil samples. The points and error bars represent the means and standard deviations of species numbers $S(n)$ for 100 random combinations of n samples ($n = 5, 10, \ldots, 120$). The fitted curve is the inverse linear function, $S(n) = S_T n/(c + n)$ with $S_T = 35$. Redrawn from Colwell and Coddington [2]

is commonly modeled by a negative exponential or inverse linear function [2], but **least squares** methods of fitting often ignore the variance structure of species counts and the interdependence of combined samples.

When n equal samples are drawn from the population, an alternative estimator that does not depend on a particular model is based on first-order **jackknife resampling**, $S + a_1(n-1)/n$, where S is the total number of species observed across all samples and a_1 is the number of species that occur in only one sample [9]. The second-order jackknife estimator,

$$S + \frac{a_1(2n-3)}{n} + \frac{a_2(n-2)^2}{n(n-1)}$$

where a_2 is the number of species that occur in just two samples, has smaller bias but larger variance [2].

Total species counts can also be estimated from a single random sample by utilizing the distribution of species abundances in the sample to estimate the number of missing species. Preston [23] suggested that the abundances of species in the population will follow a **lognormal distribution**, whence the distribution in a random sample is a Poisson

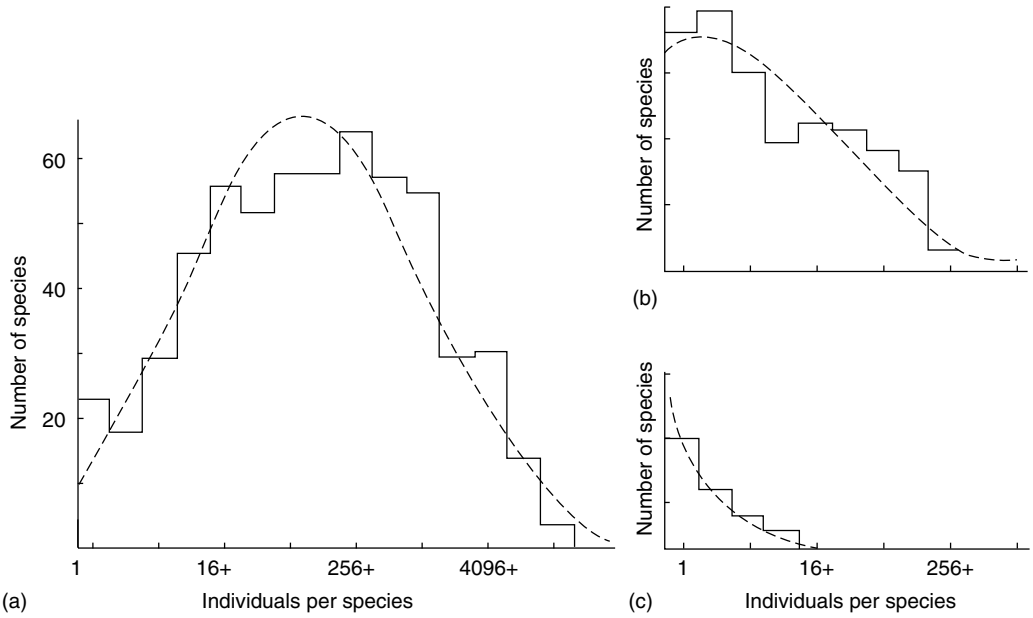

Figure 2 Lognormal fits to three **abundance** distributions (using logarithmic intervals) of moth species from annual light-trap samples with decreasing proportions of the species assemblage sampled. (a) Cumulative distribution from 225 UK sites: $N = 656\,943$ moths, $S = 585$ species. (b) Distribution for stable (woodland) site: $N = 10\,705$, $S = 205$. (c) Distribution for impoverished (urban) site: $N = 153$, $S = 38$. Redrawn from Taylor [29]

lognormal with missing zero cell [1]. Fitting the zero-truncated Poisson lognormal to the sample distribution (Figure 2) gives an estimate of the number of missing species a_0 and total species count $S_T = S + a_0$.

Both approaches to estimating the total species count suffer from the usual problems of **extrapolation**, particularly when a substantial proportion of the total species is not sampled. For example, in sampling insects from the canopy of tropical forests by using knock-down insecticides over 50% of species may be represented by only a single individual, suggesting a vast hidden reservoir of species [28]. Taylor et al. [30] found that the species accumulation curves from eight years of sampling moth species by light traps were often linear on $\log n$ [7] and showed no evidence of approaching an asymptote (Figure 3). Kempton and Taylor [12] also found that estimates of S_T from fitting the Poisson lognormal to the abundance distributions of moth species from annual light-trap samples had large variances and were poor discriminators for sites.

An alternative approach to comparing species richness that avoids the need for extrapolation is based on

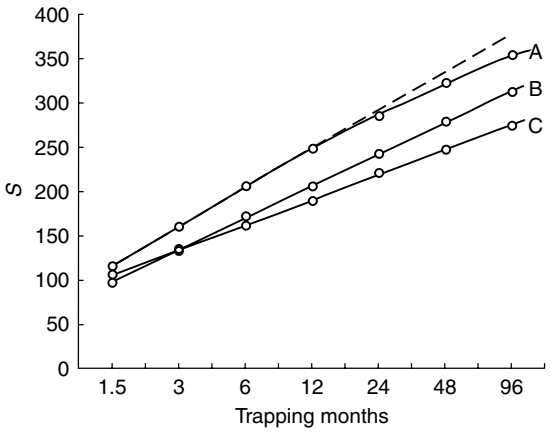

Figure 3 Species accumulation curves for eight years of sampling by light trap at three stable woodland sites in southern Britain. Individual nightly samples are pooled and then subsampled at 2-, 4-, 8-, 16-, 32- and 64-day intervals to simulate samples obtained with different sampling intensity. Note that if diversity is identified with the sample species count, S, the ordering of sites changes with sampling effort. This can be explained by the fact that the same sampling effort produced more than twice the number of individual moths in site C compared with site B. Drawn from data in Taylor et al. [30]

standardizing sample species counts to a fixed sample size by using a rarefaction technique. Suppose we collect a random sample of size N consisting of S species with abundances $N_i, i = 1, \ldots, S$. Then an unbiased estimator of the expected number of species in a smaller sample of size m is

$$\widehat{S}(m) = \sum_i \left[\frac{1 - C(N - N_i, m)}{C(N, m)} \right] \qquad (1)$$

where $C(u, v)$ is equal to $u!/[v!(u - v)!]$ for $u \geq v$ and is zero otherwise [26]. In 1979 I compared the annual totals of moth species trapped at two stable woodland sites over 10 years and found that standardizing all samples to the minimum sample size substantially reduced the annual variation in S and increased site discrimination [11]. When differences in sample size between sites are due to sampling artifacts standardization can easily be justified, but when they reflect real differences in population density the use of standardized comparisons is more debatable [5]. Nevertheless, the alternative of standardizing for sample effort is more likely to produce the inconsistencies in site comparisons observed in Figure 3.

Compound Diversity Measures

The total species count provides a very limited characterization of population variability, and substantial effort has been directed to investigating other measures. A standard measure of variability is the standard deviation of the species **abundances** or, given their observed approximation to a lognormal distribution, their log abundances. The diversity of a multispecies population might then be characterized by both the total number of species and the evenness or equitability of their abundances [21]. An alternative development has been to define compound diversity measures that are functions of the species proportional abundances π_i ($i = 1, \ldots, S_T$). Hill [10] proposed a family of such measures:

$$\Delta_r(\boldsymbol{\pi}) = \left(\sum \pi_i^r \right)^{1/(1-r)} \qquad (2)$$

where r is any real number. When $r = 0$, all species have equal weighting and $\Delta_0 = S_T$, but for positive r, Δ_r gives greater weight to the more abundant species. In particular, $\Delta_1 = \exp H$, where $H = -\sum \pi_i \log \pi_i$ is the Shannon information index, and $\Delta_2 = 1/\sum \pi_i^2$, the reciprocal of Simpson's index [25]. Both these long-standing indices have been given theoretical interpretations as diversity measures but convincing evidence of their suitability needs to come from empirical studies of the performance of their sample estimators (Table 1). Since Δ_2 and, to a lesser extent, Δ_1 are relatively insensitive to the rarer species, these measures are less affected by sample size than is the species count S, but they were found to be poorer discriminators in a study that compared between-site variation of different diversity indices with year-to-year variation

Table 1 Estimators of some diversity measures for a sample of S species with ordered abundances $N_i, i = 1, \ldots, S$, $\sum N_i = N$, with an assessment of their discriminant ability and sensitivity to sample size under a typical species abundance model [17, Table 4.5]. The discriminant ability of an index is measured by the ratio of its variance between sites to that within sites [11, Figure 2]. For the Q index, an alternative estimator for small samples is given in [15]

Index	Estimator	Sensitivity to sample size	Discriminant ability
Species richness	S	High	Moderate
Interquartile, Q	$S/[2\log(N_{0.25S}/N_{0.75S})]$	Moderate	Good
Shannon H	$\log N - \left[\sum (N_i \log N_i)/N\right]$	Moderate	Moderate
Simpson	$\left[\sum N_i(N_i - 1)\right] \Big/ \left[N(N - 1)\right]$	Low	Poor
Berger–Parker	N_1/N	Low	Poor
Shannon evenness	$H/\log S$	Moderate	Poor
Log-series α		Low	Good
Lognormal S_T		Low	Poor
Lognormal σ		Low	Poor
Lognormal S_T/σ		Low	Good

within sites [11]. In general, indices that are sensitive to the rarer species are severely affected by differences in sample size, while indices that are sensitive to the most abundant species are often poor site discriminators because of their high variability across years. This led Kempton and Taylor [13] to propose an index Q based on the middle-ranking species in the population and defined by the interquartile slope of the cumulative distribution of species log abundance, $Q = S_T/[2\log(\pi_{0.25S_T}/\pi_{0.75S_T})]$, where π_q is the proportional abundance of the qth most abundant species. The need to compromise between discriminant ability and sensitivity to sample size in choice of diversity measure was highlighted by Magurran [16]. The performance of **diversity measures** on these two criteria will depend on the form of the distribution of species abundances and the nature of their individual variability, but some guidance is given in Table 1.

An alternative, parametric approach to measuring diversity comes from empirically modeling the variability of species abundances. The parameters of the fitted distribution are then used as diversity measures. If the underlying population distribution is assumed to be lognormal, sample estimates may be derived for both S_T and the standard deviation of log abundances σ. Kempton and Taylor [12] found that these two estimates are usually highly positively correlated and, taken individually, are poor site discriminators; but their ratio, $\lambda = S_T/\sigma$, is well defined and may be equated with a constant multiple of the Q statistic. Similar results hold for the gamma distribution, a common alternative to the lognormal. In this case, if S_T and σ are large, the sample distribution approximates to a log series with single diversity parameter α. Each of the diversity measures in Table 1 can be expressed as a function of the parameters of the chosen species abundance distribution, leading to estimates that are more efficient and less dependent on sample size under the model assumptions. An important characteristic of a diversity measure is, then, the robustness of its estimate to the model assumptions, particularly when the abundance distribution is not well defined by the sample (*see* **Robust inference**).

Interpreting diversity assessments is particularly difficult when different diversity measures give different orderings of environmental sites, even after allowing for differences in sample size. Patil and Taillie [19, 20] introduced the concept of intrinsic diversity to examine whether an absolute ordering can be applied to two populations P and P' based on their species proportional abundances. P' is defined to be intrinsically more diverse than P if it can be derived from P by a sequence of two operations:

1. introducing a new species to share the abundance with a species already present;
2. transferring abundance between two species to make them more equivalent.

Intuitively, both operations raise the diversity, the first by increasing species richness, the second by increasing evenness. A necessary and sufficient condition for $P' \geq P$ is

$$\sum_{i \leq j} \pi_i \geq \sum_{i \leq j} \pi_i', \quad \forall j = 1, \ldots, \max(S_T, S_T')$$

where S_T' is the species total for population P', π_i and π_i' are the proportional abundances of the ith commonest species in populations P and P', respectively, and the vectors $\boldsymbol{\pi}$ and $\boldsymbol{\pi}'$ are filled out with zeros if necessary so that they are of equal length [27]. Hence, two populations have an intrinsic diversity ordering if their curves of cumulative species proportional abundance do not intersect.

A minimum requirement of any proposed measure of diversity is that it orders sites according to the intrinsic diversity ordering of their local populations, whenever such an ordering exists. A necessary and sufficient condition for a function $f(\boldsymbol{\pi})$ to be an intrinsic diversity measure is that

$$\left(\frac{\partial f}{\partial \pi_i} - \frac{\partial f}{\partial \pi_j}\right)(\pi_i - \pi_j) \leq 0, \quad \forall i, j$$

that is, that f is Schur concave [27]. It is easy to show that all commonly used diversity indices, including the rarefraction index (1) and Hill's family (2), are Schur concave and so will give identical orderings of a set of sites whose populations have an intrinsic diversity ordering. If the population abundance distributions at all sites follow a log-series distribution, the sites have an intrinsic diversity ordering given by the parameter α. However, if populations P and P' follow a lognormal distribution then P' is intrinsically more diverse than P if and only if $S_T' \geq S_T$ and $\sigma' \leq \sigma$, i.e. P' exceeds P in both species richness and evenness. If, however, $S_T' > S_T$ and $\sigma' > \sigma$, the diversity ordering will depend on choice of measure. For example, with Hill's family Δ_r, the populations

will be ordered on species richness for r close to zero, whereas for large r ordering is based on evenness $1/\sigma$. Likewise, Kempton and Taylor [14] explained the inconsistencies in site ordering for moth diversity, for different rarefraction indices $S(m)$, by the deviations of species abundance distributions of some sites from the log-series model.

Patterns of Diversity

Despite extensive research into diversity measures, mainly concentrated in the 1970s, most biodiversity assessment is still based on species richness. This may be explained by the general lack of information on the distribution of species abundances and the ease of interpretation of species counts.

One rich source of study has been the assessment of global biodiversity for different species groups. May [18] describes various methods of inference: extrapolation of trends in species identification since the first classification by Linaeus in 1758; direct assessment based on the overall fraction of species previously recorded among newly studied groups; indirect assessment from specialization to plant species; and estimates inferred from empirical patterns in species-size relations or **community food web** structures. These lead to a range of species estimates from 3 million to 30 million, although the breakdown of the traditional species concept for very small organisms makes any assessment here particularly questionable. Up to 2 million species are currently named but, allowing for synonyms, the total number of species so far identified is estimated at between 1.4 million and 1.6 million [28], perhaps little more than 10% of the total. The proportion of species identified varies substantially between taxonomic groups (Figure 4): for birds, Diamond [4] notes that of the 9000 or so species recorded up to 1975, only 134 had been discovered in the previous 42 years, suggesting that the current inventory is well over 90% complete; for many insect groups, however, fewer than 10% of species may yet have been recorded. The largest taxon, in terms of both identified and projected numbers, is that of beetles, which is estimated to include more than 25% of all living species.

Much interest has focused on global and regional patterns of diversity [6]. The most widely cited

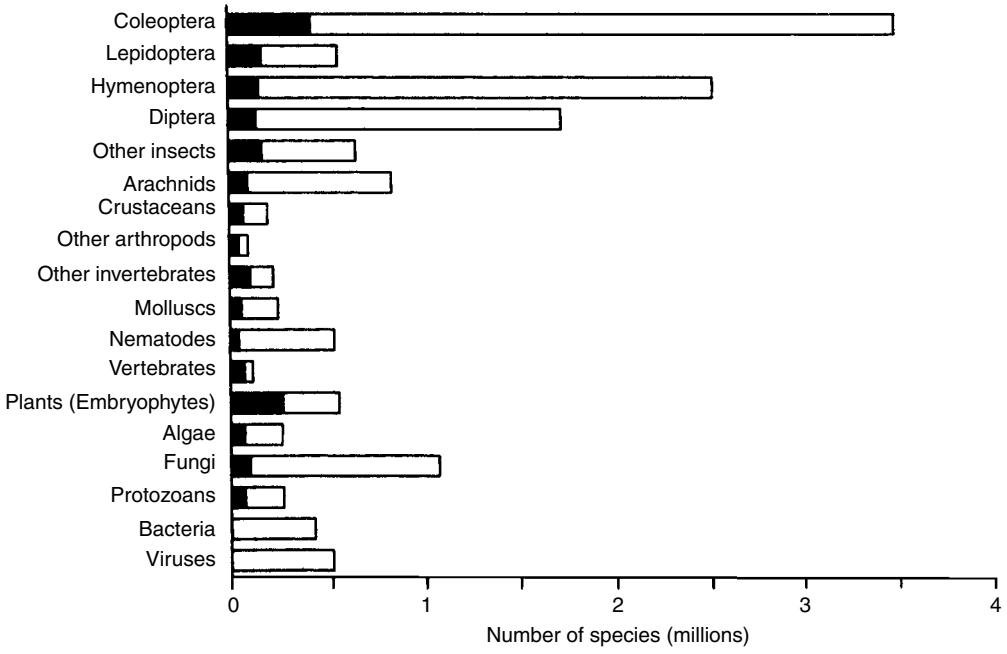

Figure 4 Global totals of species for different taxa: open bars are projected totals based on overall global estimate of 12.5 million species, shaded areas are numbers identified to date. Reproduced from Stork [28] by permission of the National Academy of Sciences

example of a direct gradient in overall taxonomic diversity relates to latitude. Overall taxonomic diversity is high towards the tropics and low towards the poles. A frequently cited explanation for this is the increase in climatic energy (measured, e.g., by potential evapotranspiration) as one moves towards the tropics, though at the regional level the effect of latitudinal trends may be masked by local factors, including habitat heterogeneity [16].

Diversity is also generally observed to be higher in low to middle elevations and in forests and to be lower at higher altitudes and in arid regions. Nevertheless, there are many examples of regions and taxonomic groups where these general observations do not hold and spatial correlations among groups are often found to be weak or nonexistent [6]. Where correlations in species richness do exist, for example in numbers of butterflies and birds among states of the US [24], they may be partly attributable to differences in habitat area. Studies of hotspots of high diversity within regions also show poor coincidence among taxonomic groups [6, 22]. Moreover, diversity hotspots do not appear to contain a higher proportion of the rarer species in a region [3, 22], which has important implications for conservation and the planning of nature reserves.

References

[1] Bulmer, M.G. (1974). On fitting the Poisson lognormal distribution to species-abundance data, *Biometrics* **30**, pp. 101–110.

[2] Colwell, R.K. & Coddington, J.A. (1995). Estimating terrestrial biodiversity through extrapolation, in *Biodiversity: Measurement and Estimation*, D.L. Hawksworth, ed., Chapman & Hall, London, pp. 101–118.

[3] Curnutt, J., Lockwood, J., Luh, H.-K., Nott, P. & Russell, G. (1994). Hotspots and species diversity, *Nature* **367**, 326–7.

[4] Diamond, J.M. (1985). How many unknown species are yet to be discovered?, *Nature* **315**, 538–539.

[5] Gaston, K.J. (1996). Species richness: measure and measurement, in *Biodiversity: A Biology of Numbers and Difference*, K.J. Gaston, ed., Blackwell, Oxford, pp. 77–113.

[6] Gaston, K.J. & Williams, P.H. (1996). Spatial patterns in species diversity, in *Biodiversity: A Biology of Numbers and Difference*, K.J. Gaston, ed., Blackwell, Oxford, pp. 202–229.

[7] Gleason, H.A. (1922). On the relation between species and area, *Ecology* **3**, 158–162.

[8] Harper, J.L. & Hawksworth, D.L. (1995). Preface, in *Biodiversity: Measurement and Estimation*, D.L. Hawksworth, ed., Chapman & Hall, London, pp. 5–12.

[9] Heltsche, J. & Forrester, N.E. (1984). Estimating species richness using the jackknife procedure, *Biometrics* **39**, 1–11.

[10] Hill, M.O. (1973). Diversity and evenness: a unifying notation and its consequences, *Ecology* **54**, 427–432.

[11] Kempton, R.A. (1979). The structure of species abundance and measurement of diversity, *Biometrics* **35**, 307–321.

[12] Kempton, R.A. & Taylor, L.R. (1974). Log-series and log-normal parameters as diversity discriminants for the Lepidoptera, *Journal of Animal Ecology* **43**, 381–399.

[13] Kempton, R.A. & Taylor, L.R. (1976). Models and statistics for species diversity, *Nature* **262**, 818–820.

[14] Kempton, R.A. & Taylor, L.R. (1979). Some observations on the yearly variability of species abundance at a site and the consistency of measures of diversity, in *Contemporary Quantitative Ecology and Related Econometrics*, G.P. Patil & M.L. Rosenzweig, eds, International Co-operative Publishing House, Burtonsville, pp. 3–22.

[15] Kempton, R.A. & Wedderburn, R.W.M. (1978). A comparison of three measures of species diversity, *Biometrics* **34**, 25–37.

[16] Kerr, J.T. & Packer, L. (1997). Habitat heterogeneity as a determinant of mammal species richness in high-energy regions, *Nature* **385**, 252–254.

[17] Magurran, A.E. (1996). *Ecological Diversity and Its Measurement*, Chapman & Hall, London.

[18] May, R.M. (1990). How many species?, *Philosophical Transactions of the Royal Society of London* **330**, 293–304.

[19] Patil, G.P. & Taillie, C. (1979). An overview of diversity, in *Ecological Diversity in Theory and Practice*, J.F. Grassle, G.P. Patil, W. Smith & C. Taillie, eds, International Co-operative Publishing House, Burtonsville, pp. 3–27.

[20] Patil, G.P. & Taillie, C. (1982). Diversity as a concept and its measurement (with discussion), *Journal of the American Statistical Association* **77**, 548–567.

[21] Pielou, E.C. (1975). *Ecological Diversity*, Wiley, New York.

[22] Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C. & Gibbons, D.W. (1993). Rare species, the coincidence of diversity hotspots and conservation strategies, *Nature* **365**, 335–337.

[23] Preston, F.W. (1948). The commonness and rarity of species, *Ecology* **29**, 254–283.

[24] Robbins, R.K. & Opler, P.A. (1997). Butterfly diversity and a preliminary comparison with bird and mammal diversity, in *Biodiversity II*, M.L. Reaka-Kudla, D.E. Wilson & E.O. Wilson, eds, Joseph Henry Press, Washington, pp. 69–82.

[25] Simpson, E.H. (1949). The measurement of diversity, *Nature* **163**, 688.

[26] Smith, W. & Grassle, J.F. (1977). Sampling properties of a family of diversity indices, *Biometrics* **33**, 283–292.

[27] Solomon, D.L. (1979). A comparative approach to species diversity, in *Ecological Diversity in Theory and Practice*, J.F. Grassle et al., eds, International Co-operative Publishing House, Burtonsville, pp. 29–35.

[28] Stork, N.E. (1997). Burtonsville, Measuring global biodiversity and its decline, in *Biodiversity II*, M.L. Reaka-Kudla, D.E. Wilson & E.O. Wilson, eds, Joseph Henry Press, Washington, pp. 41–68.

[29] Taylor, L.R. (1978). Bates, Williams, Hutchinson – a variety of diversities, in *Diversity of Insect Faunas*, L.A. Mound & N. Waloff, eds, Blackwell, Oxford, pp. 1–18.

[30] Taylor, L.R., Kempton, R.A. & Woiwod, I.P. (1976). Diversity statistics and the log-series model, *Journal of Animal Ecology* **45**, 255–271.

(*See also* **Diversity profiles**; **Population ecology**)

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