

# The introduction of species abundance distribution

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The following six Species abundance distribution (SAD) models were considered:

broken-stick, niche-preemption, log-normal, Zipf, Zipf-Mandelbrot, and neutral-theory models (Table 1). Further details and comments of other SAD models are described by McGill et al. (2007) and Wilson (1991).

**Table 1.** Six main species abundance distribution models.

Model	Equation	Reference
Broken-stick	$\hat{a}_r = \frac{N}{S} \sum_{k=r}^S \frac{1}{k}$	(1) MacArthur (1957)
Niche-preemption	$\hat{a}_r = N\alpha(1-\alpha)^{r-1}$	(2) Motomura (1932)
Log-normal	$\hat{a}_r = \exp[\log(u) + \log(\sigma)\Phi]$	(3) Preston (1948)
Zipf	$\hat{a}_r = N\hat{p}_1 r^\gamma$	(4) Frontier (1987)
Zipf-Mandelbrot	$\hat{a}_r = Nc(r+\beta)^\gamma$	(5)
Neutral-theory	$\phi_n = \theta \frac{J!}{n!(J-n)! \Gamma(J+\gamma)} \int_0^\gamma \frac{\Gamma(\gamma)}{\Gamma(1+\gamma)} \frac{\Gamma(n+y)\Gamma(J-n+\gamma-y)}{\Gamma(\gamma-y)} \exp(-y\theta/\gamma) dy$	(6) Hubbell (2001)

Note:  $\hat{a}_r$  is the expected abundance of species at rank  $r$ ,  $S$  is the number of species,  $N$  is the number of individuals,  $\Phi$  is a standard normal function,  $\hat{p}_1$  is the estimated proportion of the most abundant species, and  $\alpha, \sigma, \gamma, \beta$  and  $c$  are the estimated parameters in each model. In neutral-theory model, where  $\Gamma(z) = \int_0^\infty t^{z-1} e^{-t} dt$  which is equal to  $(z-1)!$ , for integer  $z$  and  $\gamma = \frac{m(J-1)}{1-m}$ ,  $\theta$  is fundamental diversity number,  $m$  is migration rate.

**Broken-stick model:** This model was first proposed by MacArthur (1957). Its analogy of placing  $s$ -points randomly on a line of unit length and simultaneously breaking it at those points into  $s$  lengths can be rephrased as a group of  $s$  series. The lengths of the segments represent the “niche sizes” of the species. According to the model, the expected size of the  $r$ th species, and  $\hat{a}_r$ , the expected abundance of species of species at rank  $r$ , are shown in equation (1) in Table 1. The mathematical proof of this model can be found in Pielou (1975).

**Niche-preemption model** This model was proposed by (Motomura, 1932) and assumes that the percentage of the total niche occupied by the first species is  $\alpha$ , the second species occupied a percentage  $\alpha$  of the remainder,  $\alpha(1 - \alpha)$ , and so on. The expected abundance for the  $r$ th species is equation (2) in Table 1.

**Log-normal model** A log-normal distribution is defined as a distribution whose variate conforms to the normal laws of probability. For SADs, the log-normal distribution characterizes a sample with relatively low abundance or very rare species (Matthews and Whittaker, 2014). Preston (1948) introduced the log-normal SAD by demonstrating a good fit to a large number of data sets covering a number of different communities. See equation (3) in Table 1.

**Zipf and Zipf-Mandelbrot model** The Mandelbrot model was originally developed for information systems, assessing the cost of information (Frontier, 1985). In plant communities, the presence of a species can be seen as dependent on previous physical conditions and previous species presences – these are the costs. Pioneer species have a low cost, requiring few prior conditions. 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 (Frontier, 1987). These differences between species give a Zipf or Zipf-Mandelbrot distribution, equations (4) and (5) in Table 1, respectively. The assumption is that a species is very likely to invade once its necessary conditions are met (Wilson, 1991).

**Neutral-theory model** Hubbell (2001) noted that the relative abundance of species within – and the species diversity of – a community can be explained through neutral drift of individual species abundances. The model contends that the number of individuals in a metacommunity is constant, that is, all available resources in the community are saturated. This is the zero-sum

assumption: if an individual dies and a portion of the resource becomes available, it will be immediately taken up by a new individual, and the community size remains constant. See equation (6) in Table 1.

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