

# Neutral theory

## Key concepts

- Macroecology
- Neutral fluctuations
- Null model
- Fisher's log series

## The unified theory of biodiversity and biogeography

Previously we introduced the *species abundance distribution* as a device for summarizing the distribution of individuals among species at a local site. Tree species at Barro Colorado Island were found to exhibit a long right tail, indicating dominance by a small fraction of species, the commonness of rare species, and high local diversity.

Indeed, as shown in Figure 2 the tail of the BCI data is much longer than that predicted by Robert MacArthur's "broken stick model" (a model of pre-emptive resource competition) and the log normal distribution (which Robert May explained as a statistical consequence of numerous additive random factors). We can visualize this disparity by plotting the residuals (difference between observation and model prediction) at each rank (Figure 3). What determines the long right tail of the empirical species abundance distribution remains an open question. Following this, we also saw that the accumulation of species with respect to area may be described by the law  $S = cA^z$  where  $S$  is the number of species,  $A$  is the area investigated, and  $c$  and  $z$  are fit constants. Following Rosenzweig we qualitatively explained the  $z$  coefficients of different species area curves with respect to biogeographic connectedness of islands, continental land masses (provinces), and collections of continents. However, at present we lack any coherent causal explanation of these observed *macroecological* patterns. The unified neutral theory of biodiversity and biogeography (colloquially referred to by most ecologists as "neutral theory") provides an explanation of both sets of phenomena.

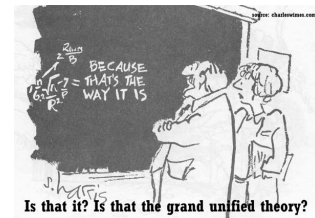


Figure 1: This chapter concerns the unified neutral theory of biodiversity and biogeography.

*Macroecology* is the theory of relationships between organisms and their environment at large spatial scales.

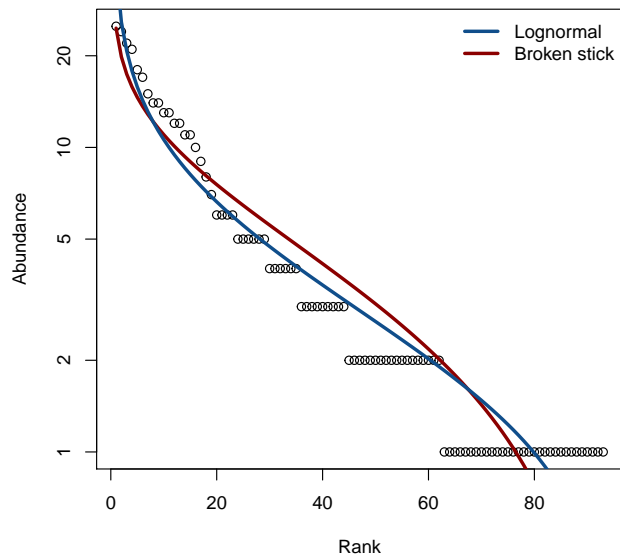


Figure 2: Species abundance distribution on a logarithmic scale for 93 tree species >10 cm dbh in a plot at Barro Colorado Island. Fit models include the broken stick (red) and lognormal (blue) models.

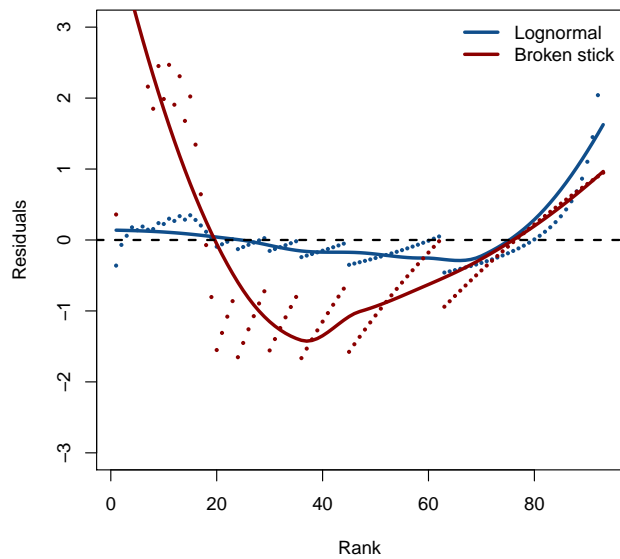


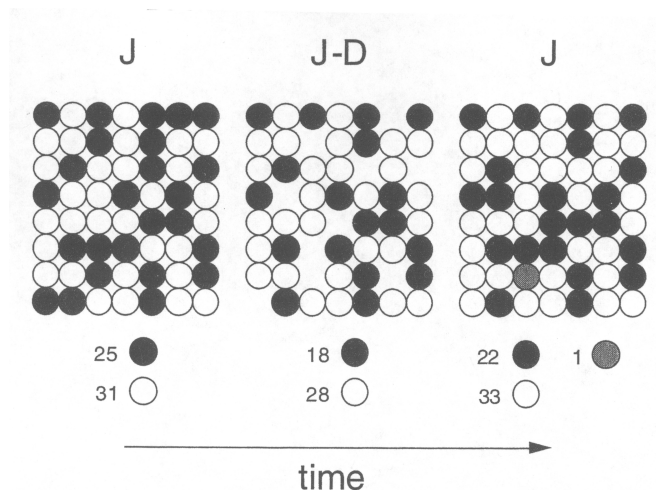
Figure 3: Residuals of fit species abundance distribution for tree species at Barro Colorado Island. A good model would have residuals evenly distributed on the zero line. This plot shows that the lognormal model fits reasonably well for dominant species. The broken stick model, by contrast, underestimates the abundance of dominant species and overestimates the abundance of mid-rank species. Both models underestimate the long right tail of the empirical species abundance distribution.

### Community dynamics of neutral theory

The chief conjecture of the neutral theory is that two processes that have so far been omitted are actually crucial to understanding diversity and are the key link between the local diversity summarized in the species area distribution and the regional diversity pattern summarized in the species area law. In outline, the neutral theory supposes that population dynamics of each species are locally independent and subject to the following rules:

- An community consists of a finite, determinite number of individuals of all species combined; the number of sites is denoted by  $J$ .
- In iterated cycles of disturbance and recruitment, individuals occupying each site are removed with probability  $p$  and replaced by recruits from from the remaining individuals with species identity given by their relative abundance in the post-disturbance community. An alternative version of the theory allows that individuals reproduce and die continuously and independently at rates  $b$  and  $d$ , respectively, assumed to be the same for all species.
- Occasionally the gap caused by disturbance or death is replaced not by a local recruit, but by an immigrant species from the surrounding metacommunity. The per capita migration rate is denoted by  $m$ .

This disturbance cycle is illustrated by Figure 4, which is reprinted from Hubbell.<sup>1</sup>



<sup>1</sup> S P Hubbell. *The unified neutral theory of biodiversity and biogeography*, volume 32 of *Monographs in Population Biology*. Princeton University Press, 2001

Figure 4: The disturbance cycle begins with a saturated community comprised of two species (light and dark sites in left panel). After disturbance, only 18 of an initial 25 individuals of the dark species remain while 28 of an initial 31 individuals of the light species remain (middle panel). Finally, after local recruitment the community is saturated again with all gaps replaced either by locally acquired recruits of the light or dark species or migration of an individual from outside the local community (right panel).

Some additional quantities are needed to fully express the model.

- The total number of individuals in the metacommunity is denoted  $J_M$ ; typically  $J_M$  will be a very large number.
- Within the metacommunity, speciation occurs at a per capita rate  $\nu$ ; typically  $\nu$  will be very small.

### *Neutrality*

Why is this theory called the unified *neutral* theory? The answer has to do with the way the number and composition of species in a community fluctuate when the model is iterated. In contrast to the resource competition intrinsic to the broken stick model and other models that postulate that species have niches, neutral theory assumes that all species have identical chances for elimination through disturbance (alternatively, identical birth and death rates). Accordingly, the model does not allow for any preferential association between species and habitats or effects of interspecific interactions. Species abundances will fluctuate in a neutral way independent of species specific traits.

Of course, this assumption is straightforward to disconfirm in nature simply by inspecting species empirical probabilities of removal by disturbance or demography. Why, then, does the theory make this simplifying assumption? One answer to this question is that it is a first order approximation. As an approximation it provides a theoretical prediction about which patterns in the distribution and abundance of species may be explained without invoking specialist theories such as the Janzen-Connell effect or the intermediate disturbance hypothesis. It therefore provides a standard against which to compare any alternative model – a *null model* with which any more elaborate theory should be prepared and the importance of the more elaborate mechanisms evaluated. Alternatively, if the neutral theory survives scrutiny then one might conclude that however much species differences may contribute to local dynamics and habitat associations, such differences do not contribute to the macroecological phenomena summarized by the species abundance distribution and species area curve.

### *Fisher's log series and solution of the neutral model*

The rules described above suffice to describe the change in species composition of a community of  $J$  individuals, given values of  $J_M$ ,  $p$  (or  $b$  and  $d$ ),  $m$ , and  $\nu$ . But what predictions does this model make? According to the neutral theory local species composition depends importantly on migration. Thus, to derive the species abundance distribution we first require information on the total number of species and their relative abundance in the metacommunity.

In 1943, statistician Ronald Fisher and biologists A.S. Corbet and C.B. Williams showed that the number of species represented by  $n$  individuals ( $S_n$ ) in a large collection of  $N$  Malayan butterflies very closely fit the equation, called *Fisher's logseries*,

$$S_n = \frac{\alpha x^n}{n}, \quad (1)$$

where  $x = N/(\alpha + N)$  and  $\alpha$  is a fit coefficient that measures diversity in small samples. (This is where the terminology of  $\alpha$ -diversity comes from.) Summing over the different values of  $n$  yields the total number of species in the community,  $S$ ,

$$S = \sum_1^{\infty} S_n = \alpha \ln \left( 1 + \frac{N}{\alpha} \right), \quad (2)$$

How does this relate to the neutral theory? From the version of the neutral theory in which births and deaths occur continuously, one can deduce that the average number of species represented by  $n$  individuals according to the neutral model is<sup>2</sup>

$$\bar{S} = \frac{S_M P_0 v (b/d)^n}{b n}. \quad (3)$$

Evidently, the neutral model predicts that species relative abundances will follow Fisher's log series with  $\alpha = (S_M P_0 v)/b$  (sometimes also written  $\theta = (S_M P_0 v)/b$ ), where  $S_M$  and  $P_0$  are unknown constants, and  $x = b/d$ . How does this relate to the species-area curve? Defining individual density as  $\rho = N/A$ , where  $A$  is the area in which  $N$  species occur, we can rearrange to obtain  $N = \rho/A$ . Substituting into equation 2 we have an equation for the species-area relationship

$$S = \alpha \ln \left( 1 + \frac{\rho}{A\alpha} \right). \quad (4)$$

In fact, this model is not equivalent to the species area curve  $S = cA^z$ , though it is very difficult to distinguish them over many orders of magnitude. For instance, the original species area curve reaches an asymptote, whereas the version based on Fisher's log series and neutral theory decelerates but does not ever stop increasing. Interestingly, attempts to determine if observed species area curves have actually reach an asymptote have failed to do so. It appears that the neutral theory may be an even better model of the species area relationship than the original species area curve itself! Using equation 4 to give the relative abundances in the metacommunity, the full model for change in the relative abundances of species in the local community

<sup>2</sup> Igor Volkov, Jayanth R Banavar, Stephen P Hubbell, and Amos Maritan. Neutral theory and relative species abundance in ecology. *Nature*, 424(6952):1035–7, August 2003. ISSN 1476-4687

may now be expressed and the average number of species represented by  $n$  individuals obtained as

$$\bar{S}_J = \alpha \frac{J!}{n!(J-n)!} \frac{\Gamma(\gamma)}{\Gamma(J+\gamma)} \int_0^\gamma \frac{\Gamma(n+\gamma)}{\Gamma(1+\gamma)} \frac{\Gamma(J-n+\gamma-y)}{\Gamma(\gamma-y)} e^{-y\alpha/\gamma} dy. \quad (5)$$

This is an intimidating formula and it is not easy to see how it can be used directly to understand species distributions and abundance! But, it has other uses. It is straightforward to program a computer to calculate it. It can therefore be used to estimate the diversity coefficient  $\alpha$ . Importantly, this equation gives rise to species abundance distributions with much longer right tails than the lognormal and broken stick models. It can even be used as the basis for formal statistical tests comparing the neutral theory with these other models. In such cases, the neutral theory has typically been shown to fit the data better.

### *Test yourself*

1. What phenomena are unified by the neutral theory?
2. What are the key processes by which species composition changes according to the neutral theory?

## *Bibliography*

- [1] S P Hubbell. *The unified neutral theory of biodiversity and biogeography*, volume 32 of *Monographs in Population Biology*. Princeton University Press, 2001.
- [2] Igor Volkov, Jayanth R Banavar, Stephen P Hubbell, and Amos Maritan. Neutral theory and relative species abundance in ecology. *Nature*, 424(6952):1035–7, August 2003. ISSN 1476-4687.