

Figure 13.1. Raw versus smoothed speciesaccumulation curves. A raw curve is produced from a particular order of samples. A smoothed curve is an average of multiple raw curves from random reorderings of the samples. Data are from 16 Berlese samples of litter-soil cores (see text).

mate the effort needed to add a particular number of species to the inventory or to increase the species list by a particular percentage. Soberón and Llorente (1993) discuss a variety of mathematical models that can be fit to species-accumulation curves. It is often the case that numerous models will fit an observed curve more or less equally well, yet diverge widely when used to make projections. The choice of a particular model must be based on assumptions about the sampling conditions. For large and poorly known faunas, Soberón and Llorente recommended the logarithmic model, in which the probability of encountering additional species declines as an exponential function of the size of the species list. With this model, the probability of encountering additional species never declines to zero, and species-accumulation curves never reach a plateau. The equation for a logarithmic curve is

$$S(t) = \frac{\ln{(1 + zat)}}{z}$$

where t is the measure of effort, such as time or number of samples; S(t) is the predicted number of species at t, and z and a are curvefitting parameters. Using the data from a smoothed species-accumulation curve (the S(t) and t values), the parameters a and z can be estimated using a nonlinear curve-fitting procedure in a statistical analysis program. For example, using the smoothed curve from the Berlese data, a fitted logarithmic curve has a = 28.46 and z = 0.023. The fitted curve is nearly identical to the smoothed curve $(r^2 >$ 0.99).

Longino and Colwell (1997) modified the logarithmic equation to

$$t_s - t_{s-1} = \frac{e^{zs} - e^{z(s-1)}}{za}$$

This equation shows the number of samples (or other measure of effort) needed to add the sth species to the inventory. At 107 species, the number obtained in the 16 Berlese samples, the cost of adding another species is still less than one additional sample, but it is increasing rapidly (Fig. 13.2). Looking at inventory progress in this fashion allows one to develop "stop-rules," invoked when the cost of adding an additional species rises above some threshold.

Other models of species-accumulation assume that the probability of encountering additional species in an inventory eventually reaches zero. These asymptotic models can be used to estimate species richness, and they are discussed in the section on richness estimation.