

Figure 13.9. Michaelis-Menten estimates of species richness based on the Berlese data. The richness estimate is the asymptote parameter of the fitted M-M equation (see text). The pooled quadrat plot shows a gradual increase in the estimate with increasing sample size. The plotted M-M curve is based on the full data set of 16 samples. Note that although it fits reasonably well, it is "cupped" relative to the observed curve, overshooting early in the curve and undershooting at the end of the curve. This is commonly observed when M-M curves are fit to species-accumulation curves.

such as the logarithmic (Coddington, pers. comm.). Also notice that the pooled-quadrat plot of the M-M richness estimate is not stable, gradually rising as sample size increases (Fig. 13.9). A difficulty with fitting asymptotic curves is that there are many different asymptotic equations and multiple methods of fitting curves to them. This results in a plethora of different estimated richness values for the same observed species-accumulation curve. Which of the different equations or curve-fitting methods is best is unknown, and it may vary from study to study (Colwell and Coddington 1994). Examples of the use of the M-M equation to estimate species richness include Clench (1979) for Lepidoptera, Coddington et al. (1996) and Silva and Coddington (1996) for spiders, and Chazdon et al. (1998) for rainforest trees.

A common richness estimation procedure is to fit relative abundance data to a lognormal curve (see the earlier section on relative abundance distributions) and then estimate the area under the "hidden" portion of the curve (Fig. 13.7). The problems of fitting a continuous distribution to discrete data (witness the drastically different distribution shapes in Fig. 13.8 and imagine how different the richness estimates would be) and the lack of a method for calculating confidence intervals for the estimates (Pielou 1975) argue against its use in most cases (Colwell and Coddington 1994; Silva and Coddington 1996).

Some nonparametric methods show promise for richness estimation. These methods have been developed for the general problem of taking a sample of classifiable objects and estimating the true number of classes in the population (Bunge and Fitzpatrick 1993; Colwell and Coddington 1994). In ecology, such methods have been most frequently applied to estimating population size from mark-recapture data. Estimating richness is essentially the same problem, with the abundance of a species in a sample equivalent to the number of captures of an individual in a mark-recapture study.

A commonly used nonparametric estimator is the first-order jackknife (Burnham and Overton 1978, 1979; Heltshe and Forrester 1983; Colwell and Coddington 1994). The estimate of species richness ( $S^*_{jack}$ ) is based on the number of uniques (L, species occurring in one sample):

$$S^*_{\text{jack}} = S_{\text{obs}} + L\left(\frac{n-1}{n}\right)$$

where  $S_{\rm obs}$  is the observed number of species and n is the number of samples. Belshaw and Bolton (1994a) use  $S^*_{\rm jack}$  to estimate the species richness of litter-soil ants in Ghana.

Chao and colleagues developed a set of nonparametric methods for estimating the number of classes in a sampling universe (Chao 1984, 1987; Chao and Lee 1992; Chao et al. 1993;