Some biological communities, such as islands and ponds, have well-defined boundaries. But most communities are not precisely defined, and so the richness of the community cannot be either. Because sampling is often area based (using, e.g., quadrats, or sampling distributed along transects), as sample size increases the area sampled does too. Ultimately this is a species-area phenomenon, and one expects species richness to be an ever-increasing function of sample area (Rosenzweig 1995). However, it may be appropriate to treat communities as though they were discrete. Colwell and Coddington (1994) take this approach, proposing that biodiversity be partitioned into two parts: the species richness of local communities and the complementarity—the dissimilarity—among these communities. When discrete, bounded communities are assumed, species-accumulation curves rise owing to increasingly accurate sampling, not species-area effects, and species richness is considered a finite community parameter.

A desirable attribute of a richness estimator is that it be independent of sample size (above some minimum sample size). For example, if one treats sample species richness as an estimator of community richness, then a species-accumulation curve shows how the estimator changes with sample size. If the curve is still climbing, then sample species richness is an underestimate of community species richness. If the curve has stabilized (reached an asymptote) above a particular sample size, then sample species richness is deemed an adequate estimate of community species richness for that sample size. Pielou's pooled quadrat method (Pielou 1966, 1969, 1975; generalized by Magurran 1988; applied by Lamas et al. 1991; Colwell and Coddington 1994) is a generalization of this approach to any richness estimator (or any index of diversity). To use the method, calculate the richness estimate based on the first sample, then on the first two samples pooled, then on the first three samples pooled, and so

forth. Plot the estimate as a function of number of pooled samples. Just as a raw species-accumulation curve can be smoothed by repeatedly randomizing sample order and averaging the curves, the estimate curve can be the average of many randomized sample orders.

A well-behaved estimator will level off, even as sample size is increasing. An objective of biodiversity research is to identify richness estimators that rise and level off sooner than sample species richness. If such estimators can be found, community species richness might be estimated with less sampling effort.

There are three general methods of estimating species richness from sample data: extrapolating species-accumulation curves, fitting parametric models of relative abundance, and using nonparametric estimators (Bunge and Fitzpatrick 1993; Colwell and Coddington 1994; Gaston 1996). In the earlier section on measuring the rate of species capture in an inventory, fitting equations to species-accumulation curves was discussed. If the equation is asymptotic, the asymptote of the fitted curve can be used as an estimate of the species richness of the community. An equation commonly used to estimate species richness is the Michaelis-Menten (M-M) equation (Clench 1979; Soberón and Llorente 1993; Colwell and Coddington 1994; Chazdon et al. 1998):

$$S(n) = \frac{S_{max}\, n}{B + n}$$

where $S(n)$ is the observed number of species, n is the number of samples, and S_{max} and B are fitted constants. When the smoothed species-accumulation curve of the Berlese data are fitted to this equation, S_{max} = 141 species (Fig. 13.9). Notice that the fitted M-M curve tends to deviate from the observed curve by overshooting at the beginning and undershooting at the end. This is a common observation (Silva and Coddington 1996), because many species-accumulation curves seem to better fit non-asymptotic curves