Lee and Chao 1994). Colwell and Coddington (1994) and Chazdon et al. (1998) evaluated these methods when applied to the problem of estimating species richness from biological data sets. Two estimators that show considerable promise are Chao2 and the incidence-based coverage estimator (ICE). Both rely on incidence (presence-absence) data. Chao2 is the simpler to calculate:

$$S^*_{\text{chao2}} = S_{\text{obs}} + \frac{L^2}{2M}$$

where L is the number of uniques and M is the number of duplicates. Calculating ICE is more complicated (Lee and Chao 1994; Chazdon et al. 1998), but it is one of the estimators provided in Colwell's EstimateS program (Colwell 1997). Chazdon et al. (1998) found Chao2 and ICE to perform similarly, although ICE was less sensitive to spatial patchiness.

When applied to the Berlese data, the pooled quadrat plot for S^*_{chao2} shows the estimate steadily increasing with sample size (Fig. 13.10). This indicates that this fauna is still far undersampled and that attempting a richness estimate at all is probably premature without additional sampling. It cannot be emphasized enough that obtaining reliable estimates of species richness from diverse communities is difficult, requiring intensive sampling effort and very large sample sizes.

Are There Patterns of Association among Samples?

When comparing different habitats, seasons, potential conservation units, and so on, one wants to know how different the communities are in species composition. For example, we may know from richness estimation that one community is depauperate relative to another. We may wish to determine whether the depau-

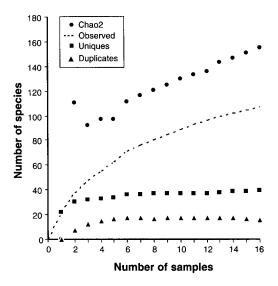


Figure 13.10. Chao2 estimates of species richness based on the Berlese data. The pooled quadrat plot shows a steady increase in the estimate with increasing sample size, which suggests that this data set is inadequate to estimate richness. The number of uniques is not declining (the presence of declining uniques is another indication of an inventory nearing completion). The number of duplicates is showing a slight tendency to decline.

perate community contains a subset of the species in the richer community or a distinct set of species.

Numerous measures of similarity and difference exist in the ecological literature (Pielou 1984; Ludwig and Reynolds 1988). A frequently used index of similarity is Jaccard's index, which is the number of species shared by two species lists (the intersection of the lists) divided by the total number of species in both lists (the union of the lists). Thus when lists have entirely distinct faunas, with no overlap, Jaccard's index equals 0, and when the two lists are identical, Jaccard's index equals 1. A measure of dissimilarity is the number of species unique to one or the other of two lists (comple-