Estimating terrestrial biodiversity through extrapolation

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SUMMARY

Both the magnitude and the urgency of the task of assessing global biodiversity require that we make the most of what we know through the use of estimation and extrapolation. Likewise, future biodiversity inventories need to be designed around the use of effective sampling and estimation procedures, especially for 'hyperdiverse' groups of terrestrial organisms, such as arthropods, nematodes, fungi, and microorganisms. The challenge of estimating patterns of species richness from samples can be separated into (i) the problem of estimating local species richness, and (ii) the problem of estimating the distinctness, or complementarity, of species assemblages. These concepts apply on a wide range of spatial, temporal, and functional scales. Local richness can be estimated by extrapolating species accumulation curves, fitting parametric distributions of relative abundance, or using non-parametric techniques based on the distribution of individuals among species or of species among samples. We present several of these methods and examine their effectiveness for an example data set. We present a simple measure of complementarity, with some biogeographic examples, and outline the difficult problem of estimating complementarity from samples. Finally, we discuss the importance of using 'reference' sites (or sub-sites) to assess the true richness and composition of species assemblages, to measure ecologically significant ratios between unrelated taxa, to measure taxon/sub-taxon (hierarchical) ratios, and to 'calibrate' standardized sampling methods. This information can then be applied to the rapid, approximate assessment of species richness and faunal or floral composition at 'comparative' sites.

1. INTRODUCTION

Extrapolating from the known to the unknown, from the past to the future, is a familiar and essential process in those biological disciplines traditionally involved in public policy, but seems rather alien to many of the kinds of biologists whose expertise is pivotal to the scientific study of biodiversity. Experimentation and mechanistic hypothesis-testing, not empirical estimation, lie at the heart of most research in contemporary genetics and ecology. In systematics, although experimentation cannot play such a central role, phylogenetic hypotheses are increasingly based on logical and quantitative criteria. Even in these cases, however, reliable methods to interpolate and extrapolate, for instance, from the few species included in an analysis to the entire higher taxon they exemplify, have been little assessed.

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The urgent challenges of global climate change, massive habitat transformation, and the threat of widespread extinction, however, have made extrapolation and prediction a crucial component of many research agendas in these fields. In the case of terrestrial biodiversity (including freshwater habitats), a reasonably accurate picture for many groups of vertebrate animals, most plants, and a very few groups of showy insects can be developed by integrating biogeographic information from faunistic and floristic surveys with the taxon-focused work of systematists (Groombridge 1992). This body of knowledge has accumulated largely under its own momentum from thousands of independent sources.

In contrast, our present state of taxonomic and biogeographic knowledge for most other groups of terrestrial organisms is sketchy at best, especially for the 'hyperdiverse' terrestrial groups: insects, mites and other arachnids, nematodes, fungi and microorganisms. Relying solely on traditional approaches, the current trajectory points to an adequate, worldwide picture for these groups no sooner than a few centuries from now (May 1990; Hawksworth 1991; Hammond 1992). (Of course, our ignorance of the true richness of these taxa makes any such projection very rough indeed.)

Clearly, then, while aggressively building human and institutional capacity in systematics (Gaston & May 1992; Anonymous 1993; Janzen 1993), approximate methods must be used to gain any useful sense of the richness, taxonomic diversity, and geographic patterning of the hyperdiverse groups. In terms of biochemical diversity and the variety of potentially useful 'evolutionary inventions' that natural selection has produced, the hyperdiverse groups present vast numbers of unexploited opportunities for furthering human welfare and solving environmental problems (Farnsworth 1988; Eisner 1990; Colwell 1992; Wilson 1992; Reid *et al.* 1993).

Moreover, it seems only logical that the most diverse groups of organisms should play a significant role in planning for the conservation and sustainable use of worldwide biodiversity (Brown 1991; Hawksworth 1991; Kremen *et al.* 1993), yet they have so far been largely ignored. Reliance only on data from a few well-known taxa such as birds, mammals, trees, butterflies or ants (e.g. Raven & Wilson 1992) assumes that variation in diversity of these groups is closely concordant with the diversity of unrepresented groups. If variation in important producer or decomposer diversity does not significantly correlate with bird diversity, for example, land-use decisions based on bird data may manage for bird diversity but against other taxa. From the point of view of an invertebrate zoologist, mammals and birds are fairly similar: mainly recent radiations of large, homeothermic heterotrophs. In contrast, the vast majority of other taxa have very different ages, histories, and lifestyles. Initial work on this question suggests that diversity patterns vary widely between taxa, and that relying on just a few groups would not optimally preserve others (Prendergast *et al.* 1993). More research on correlations between well-known but depauperate lineages and hyperdiverse groups is urgently needed before the 'indicator group' strategy is widely applied.

In this paper, we will focus first on how terrestrial biodiversity is organized, then on methods of estimation and extrapolation. Some of the methods we will discuss have been widely used to develop quantitative estimates of terrestrial species richness, yet some promising quantitative techniques, such as non-parametric estimators of local species richness, have been little used.

As for actual numerical estimates of global terrestrial species richness, we direct the reader to the plethora of recent reviews and debates on this subject (May 1988, 1990, 1992; Stork 1988, 1994; Gaston 1991; Hawksworth 1991; Hodkinson & Casson 1991; Hammond 1992; Wilson 1992). Although estimating global species richness has attracted much attention, further progress on this front awaits a better understanding of the structure and variation of biodiversity on smaller scales, especially in landscapes or 'park-sized' units. Moreover, land-use decisions are most often made at these levels and have great impact on the long-term future of biodiversity.

2. THE ORGANIZATION OF TERRESTRIAL BIODIVERSITY

Imagine a magnificent and omniscient Geographic Information System (GIS) for all the Earth's living species, with the capacity to display any level of the Linnean hierarchy on any spatial scale, for any season of the year. To take an avian example that could actually be approximated with present knowledge, we might request that the distribution of the family Trochilidae (hummingbirds) be superimposed on the world map, indicating either absence of the family or the presence of one or more of the *ca.* 320 known species of hummingbirds. Virtually all of the New World continental land masses would light up (hummingbirds are strictly a New World group), from southern Alaska and central Canada to the tip of Tierra del Fuego, plus the Antilles and Juan Fernandez archipelagos (Blake 1953; De Schauensee 1970; Land 1970; Skutch 1973; Tyrrell & Tyrrell 1985; Colwell 1989; Ridgely & Gwynne 1989; Stiles & Skutch 1989; Tyrrell & Tyrrell 1990).

A species density map ('topographic' contours showing the number of hummingbird species at each point on the map) would display a gradient from the lowland tropics, where the ranges of a dozen or more species often overlap, toward single species at the northern and southern ends of the family range (Skutch 1973; Feinsinger & Colwell 1978; Stiles 1980). Zooming in on Central America, and then on Costa Rica would reveal further 'fine-structure' of species density, from five species recorded from 3100 m elevation at Cerro de la Muerte (Colwell 1973; Wolf *et al.* 1976), to 14 species at 1400 m at Monteverde (Feinsinger 1976, 1978), to 25 species at La Selva Biological Station in the Atlantic lowlands (Stiles 1980; Karr *et al.* 1990). If we next request seasonal maps, however, we would see that some of the species

at each site are year-round residents, whereas others are seasonal migrants, dependent on seasonal nectar sources not only at those sites but at other elevations or latitudes. Some of the species are found at only one of the three Costa Rican sites (among other places) and some are found at two of them. (None occurs at all three.) Finally, if we requested full geographic range plots, species by species, for the hummingbirds at these three sites, we would find that some are endemic to Costa Rica and Western Panama, some extend as far north as Arizona, and others as far south as the Amazonian basin.

This complex mix of wide-ranging and narrowly endemic species, of different patterns of seasonality, with broad latitudinal and elevational gradients of local species richness is absolutely characteristic of terrestrial organisms: not only birds, but other vertebrates, insects, arachnids, plants, and no doubt fungi, protists, and bacteria as well. Moreover, the same kinds of patterns are repeated in many forms and at many scales. Local assemblages of herbivorous insects or mites are characteristically a mixture of host plant specialists and generalists, and the same is true for parasitic organisms in relation to their hosts (Futuyma & Moreno 1988). Pollinator assemblages include everything from obligate, one-to-one relationships with plants (e.g. figs and fig wasps), to broad generalists that pollinate dozens or even hundreds of plant species (Real 1983). Rainforest arboreal mite communities show the same kinds of complex geographical patterning as the hummingbirds in the example above, but also display striking faunal differences on a scale of meters, from forest floor, to tree trunks, to leaves (Walter *et al.* 1994).

3. RICHNESS AND COMPLEMENTARITY

(*a*) *Concepts*

The omniscient GIS imagined above represents the true global pattern of biodiversity (from the species level on up) that any estimation scheme should be designed to approximate. For the best-known groups, such as birds, mammals, or butterflies, species-by-species patterns may be developed to estimate local species richness and patterns of biogeographical overlap, as in the hummingbird example. For the hyperdiverse groups, in contrast, exhaustive inventory on a broad geographical scale is out of the question. Even the 'All Taxon Biological Inventories' (ATBIS) now being discussed (Janzen & Hallwachs 1993; Yoon 1993) will require, at least, interpolation between sampled points along habitat gradients for the smallest and most diverse organisms, and very likely a variety of approximate methods for the sampling points themselves. For plants, records are still sufficiently poor for some regions, especially tropical forests, that we will need to rely on similar kinds of sampling and estimation for the foreseeable future (Raven 1988).

As an idealized (and much-used) design for a component study in a regional biological inventory, imagine a series of local species inventories at 'points' spaced along a gradient, or located randomly within a habitat mosaic. For example, in a study of freshwater fishes or algae, the points might be sampling stations spaced along the gradient from the headwaters of a river to its estuarine mouth. For plants or birds the gradient might be an elevational transect from temperate deciduous forest to alpine tundra, with a 4 ha plot every 500 m elevation; or the tropical equivalent. Or, the gradient might, instead, be a forest chronosequence, from early to late succession. As another temporal example, the 'points' might be a series of malaise trap samples of flying insects taken in the same trap over a 'gradient' from dry season to wet season in a tropical deciduous forest. Alternatively, the 'points' might be tree species in the biochemical mosaic of a rainforest, for a study of herbivorous insects. On a global scale, each 'point' might be a 50 000 ha ATBI site covering a range of macrohabitat gradients, as a component of a series of ATBIS placed within different phases of the worldwide mosaic of major biomes (Solbrig 1991; di Castri *et al.* 1992*a*,*b*; Vernhes & Younès 1993; Yoon 1993).

In each of these cases (and many more), the problem of gaining an approximate description of the pattern of biodiversity for some taxon along a gradient or among the phases of a mosaic can be broken down into two parts: measuring or estimating the species *richness* of species assemblages locally, and measuring or estimating the *complementarity* – the distinctness or dissimilarity – of these local inventories.

The concept of complementarity is intended to cover distinctness in species composition over a broad spectrum of environmental scales, including small-scale ecological differences, such as the differences between the mite faunas of the trunk versus the leaves of a single tree species (Walter *et al.* 1994); between-habitat and landscape-level differences along environmental gradients ('beta diversity' or 'species turnover') (e.g. Shmida & Wilson 1985; Palmer & Dixon 1990); faunistic and floristic differences between distant sites in the same biogeographic realm; and (at the level of higher taxa) climatically analogous sites on different continents or even climatically distinct sites in different biomes. This broad use of the term 'complementarity' extends Vane-Wright's usage for comparing the biota of potential reserves (Vane-Wright *et al.* 1991; Pressey *et al.* 1993).

We prefer a single, broad term to a series of more specific, scale- or gradient-dependent concepts, to emphasize that the problem of characterizing differences in the species composition of component assemblages is both universal and crucial to the subject of estimating biodiversity, regardless of causal mechanism and of spatial or temporal scale. Using the concept of complementarity, when appropriate and informative, in place of its logical opposites, similarity or overlap, allows us to see both local richness and biotic (floral or faunal) differences as positive components of biodiversity. (Biotic similarity is negatively related to overall biodiversity.) The choice of complementarity over its statistical

equivalents, distinctness, dissimilarity or distance, is strictly a rhetorical preference, to capture the sense that complementary faunas or floras form parts of a whole: a sense that distinctness (or its equivalent) does not convey.

(*b*) *Optimizing complementarity in inventories*

Local richness and complementarity interact in complex and vexing ways (as we will discuss below), but treating them as separate components of biodiversity helps reveal common threads and common pitfalls in the methods that have been used to estimate biodiversity, and may aid in designing efficient inventories (Longino 1994) and in developing strategies for conservation (Pressey *et al.* 1993).

Measuring biodiversity in terms of the components due to the species richness of local assemblages and the complementarity between them does not require the world to follow any particular model of community or landscape structure, but it does mean making decisions about how to define the units to be inventoried and compared. As a first approximation for this step, there is rarely any better strategy than relying on the informed intuition of experienced naturalists. For a regional inventory of rainforest trees, for example, perhaps over a 10 000 ha area, units might be defined by the intersection of factors based on life zones, major soil types, gap phases, slope, and elevation above sea level, with replicate plots or transects placed within each inventory unit. In any inventory, if preliminary data show that the species composition of adjacent inventory units along a transect, or of the phases of a mosaic, are quite similar, the spatial or ecological scale might safely be made coarser. On the other hand, if these units prove to have largely distinct species lists, the scale might have to be made finer to gain a reasonable picture of the full biota of the region for some taxon.

The optimal spatial or ecological scale of inventory units clearly depends crucially on the biology of the organisms to be sampled, as well as the size of the project budget. Birds and beetles obviously respond to different environmental features on different scales, and so do hawks versus hummingbirds, and dung beetles versus weevils. In addition to specifying sampling or census methods, inventory protocols need to be specific about the scaling of inventory units. Often, scaling compromises will be made in the interest of simplifying inventory protocols so that each protocol covers the broadest taxonomic spectrum feasible. It is beyond the scope of this paper to make even a rough attempt to specify scales or protocols for particular target taxa, or to review the enormous taxon-specific literature on sampling methodologies. Although significant efforts have been made to develop 'portable' inventory protocols that provide reliable results among biomes and continents (e.g. Gadagkar *et al.* 1990; Hammond 1990; Coddington *et al.* 1991; Stork 1991; Heyer *et al.* 1993), much remains to be done, especially for the hyperdiverse taxa.

When methods to estimate local richness and complementarity, including their confidence intervals, are more fully developed, integrated, and tested, the cost of inventorying should favour allocating sampling effort as thinly and widely as possible, consistent with the degree of accuracy in the complementarity estimate required. At present, it is unclear which groups scale geographically at similar rates. For large-scale inventories, each major taxon is likely to require a distinct inventory strategy.

4. ESTIMATING LOCAL RICHNESS BY SAMPLING

Measurement of local richness by complete census is feasible, in the terrestrial realm, only for plants and perhaps for conspicuous and highly philopatric mammals (e.g. territorial primate troops). Even for these groups, estimation by sampling may nonetheless be the best option, but for virtually all others, measurement means sampling. Traditional collection methods employed in floral or faunal surveys by professional collectors for museums and herbaria may intend to collect all species, but such a goal is notoriously difficult either to attain or monitor.

Suppose the goal of an insect faunal study is to collect and mount a 'series' of 20 individuals for every species of leaf beetle (Chrysomelidae) at a site. Whether collecting is done by examining leaves, by sweep-netting, or by using traps, at the start of the survey every leaf beetle is part of the sampling universe, and every one is collected. Sampling is uniform – and species-blind – with regard to individual leaf beetles discovered. Under the most optimistic scenario, the sampling universe is simply contracted by one species every time a series

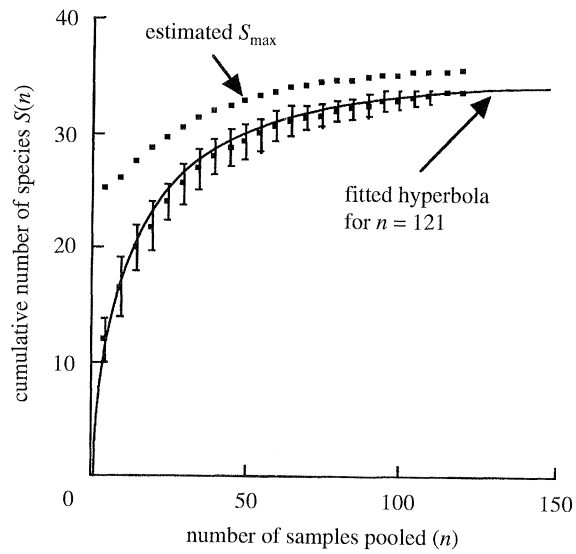

Figure 1. Collector's curve for seedlings germinating from 121 soil samples. Each point in the lower set of points represents the mean of 100 randomizations of sample pooling order; error bars are the corresponding standard deviations. (Only every fifth point is shown.) The hyperbola was fitted using means for all 121 values of n, using the maximum likelihood method of Raaijmakers (1987). The upper set of points shows the maximum likelihood estimates of S_{max} for successively larger subsets of the data.

reaches 20 individuals; all subsequent individuals of that species are ignored, and sampling continues, uniformly directed at all remaining species. This assumes that the collector can accurately identify all individuals prior to collecting them, an ideal approached in very few hyperdiverse groups. In practice, even the most exhaustive methods, applied over substantial periods of time, will leave many species with 'short series' of less than 20 individuals, and in all likelihood a number of species will be represented only by one specimen: the 'singletons'. Unfortunately, a substantially incomplete survey looks very much the same as a substantially complete one, in terms of the persistence of singletons and incomplete series for rarer species.

How can we tell, then, if the survey is essentially complete, given that the objective of a series of 20 of each species has not been met? If little can be gained by further sampling, it would be a waste of time and money to continue, but if many species characteristic of the site remain to be discovered there, more effort is called for, particularly if the species list is to be compared with other sites to assess complementarity. To put the question another way, how much additional effort would have to be invested, or how many additional beetles would have to be examined, to bring the survey to some specified level of completeness at the site?

(*a*) *Extrapolating species accumulation curves*

A 'species accumulation curve', or 'collector's curve', is a plot of the cumulative number of species discovered, $S(n)$, within a defined area, as a function of some measure n of the effort expended to find them (figure 1). The most straightforward measure of effort is simply the number of individuals (or ramets) examined, but since this means continuing to count individuals of species already discovered, as well as those that represent new species, it is not likely be useful for traditional 'museum' collecting. Instead, effort may be represented by a proxy for individuals, such as the cumulative number of samples, area of quadrats, mass of medium processed (e.g. soil or water volume) or of biomass sampled, hours of observation, number of trap-days, metre-days of mist net exposed, etc.

In the botanical literature, both the functional equivalent of species accumulation curves, used for estimating local richness (Palmer 1990), and regional-scale species accumulation curves are referred to as 'species–area curves'. Although no habitat is truly homogeneous, in what follows we will use the term 'species accumulation curve' to refer to a data set for a local species assemblage in an area of habitat that is roughly homogenous, both spatially and temporally, reserving the term 'species–area curves' for large-scale biogeographic patterns comprising explicitly heterogeneous areas. (Later, we will suggest a way to determine whether a species accumulation curve represents adequately homogenous samples.) Sampling over gradients in time is logically similar to sampling over gradients in space. A point estimate of 'local richness' should be local in time as well as space.

In theory, species accumulation curves based on 'proxy' units such as trap-hours or hours of observation represent a uniform process: as only new species increment the curve, progressive restriction of the collector's attention to species remaining to be discovered introduces no bias. For example, examining the contents of a randomized series of traps for new species, using number of traps examined as the measure of 'effort', should represent a uniform process even though the actual effort to examine each sample may decrease later in the series when most species have been discovered. In the case of unstandardized observational studies or *ad hoc* collecting, however, not only individuals of already discovered species, but also their habitats and activity times (for animals) tend to be neglected once they are discovered, biasing the process if hours or other times units are used as a measure of effort.

As an example, figure 1 presents a species accumulation curve from a seed-bank study in a 16 year-old secondary forest stand at La Selva Biological Station in Costa Rica (B. Butler & R. L. Chazdon, unpublished data). Altogether, 121 standardized soil samples were collected on a 10 m × 10 m grid covering 1 ha. The lower set of points in figure 1 shows the cumulative number of species of seedlings, $S(n)$, that germinated from soil samples in a shadehouse, plotted against n, the number of samples pooled. In this study, a complete list of the individuals that germinated from each sample was compiled, by species, generating a species-by-samples abundance table. Because the samples were all collected at once and were intended to represent ecologically random points within the plot, the order in which the samples are accumulated to produce the curve is logically arbitrary.

In all species accumulation curves, the order in which samples are added to the total affects the shape of the curve. Variation in curve shape due to accumulation order arises from sampling error, as well as from real heterogeneity among the units sampled. To eliminate this arbitrariness, the sample order may be randomized. For the seed-bank study, sample order was randomized 100 times and the mean and standard deviation of $S(n)$ computed for each value of n between 1 and 121. (The means were quite stable after around 20 randomizations.) The lower curve in figure 1 shows these mean values (as points) and their standard deviations (as error bars).

Even when samples have some intrinsic ordering (such as time series or quadrats along a transect), randomization of sample order still makes sense as long as the samples themselves are reasonably homogeneous, given sampling error. One way to examine the level of homogeneity is to compare the empirical mean randomized species accumulation curve with the curve expected if the individuals in all samples pooled had been randomly assigned to the samples. If this expected curve rises significantly more steeply from the origin than the mean empirical curve, then the empirical samples are more heterogeneous in species composition than sampling error, alone, can account for.

There are two ways to compute the expected curve

and its standard deviation directly from the relative abundance of species in the pooled samples. One can either compute a rarefaction curve (the sampling-without-replacement version) (Heck *et al.* 1975; Simberloff 1979; Tipper 1979; James & Rathbun 1981) or a 'random placement curve' (Coleman 1981; Coleman *et al.* 1982), in either case using the mean number of individuals per empirical sample (call it Y) as the sample size for each theoretical sample. For n samples of Y individuals each, the rarefaction approach assumes n random draws of exactly Y individuals from the pooled samples, whereas (for this application) Coleman's random placement approach assumes that all nY individuals are assigned at random to n collections. For either approach, a complete species-by-sample matrix of species abundances is required.

For the seed-bank data, the rarefaction and random placement curves (and their standard deviations), computed in this way, are virtually identical. We have not explored whether this similarity is intrinsic (given this particular adaptation of the methods), or data-dependent. (The random-placement curve is far more efficient computationally.) In any case, the empirical mean accumulation curve for the seed-bank data matches the theoretical curve moderately well, lying, at most, no more than 1.7 standard deviations below it.

When a species accumulation curve can be reasonably justified as representing a uniform sampling process for a reasonably stable universe, as in the seed-bank example, extrapolation becomes a logical possibility, and a statistical challenge. Two general categories of functions have been used to extrapolate species accumulation curves: asymptotic and non-asymptotic.

In the earliest example we have been able to unearth of the use of an asymptotic curve, Holdridge *et al.* (1971) censused and mapped trees in 0.1 ha plots at 46 sampling sites in different climate zones of Costa Rica. Because the number of plots varied from 1 to 11 per site, and tree species richness between 20 and nearly 100, they sought some way to compare species richness among sites. At each site, the maps for all plots were subdivided into the maximum number of subplots of $n = 200$, 400, 600, 800, 1000, 2000, 3000, 4000, and 5000 m^2, and the number of tree species $S(n)$ in each subplot was recorded. True tree species richness S_{max} for each site was then estimated by fitting the resulting mean values of $S(n)$ for each subplot size n at that site to the asymptotic, negative exponential function

$$S(n) = S_{max}(1 - e^{-Kn}), \tag{1}$$

where S_{max}, the asymptote, is the estimated true richness for the site, and K is a fitted constant that controls the shape of the curve.

The species accumulation curves and the estimates of species richness produced by Holdridge *et al.* (1971) form a crucial component of their classic study, in spite of the approximate nature of the estimates. The method they devised for sub-sampling the plots to estimate $S(n)$ is equivalent to the randomization procedure used in figure 1. Soberón & Llorente (1993) have derived a negative exponential version of a general model for species accumulation curves, pointing out that the negative exponential assumes that the probability that the next individual represents a new species depends linearly on the current size of the species list, decreasing to zero as the asymptote is approached. Miller & Wiegert (1989) also used this model to estimate species richness asymptotes.

A second asymptotic model for species accumulation curves is the two-parameter hyperbola,

$$S(n) = \frac{S_{max}\, n}{B + n}, \tag{2}$$

where S_{max} and B are fitted constants; the curve passes through the origin. This function, as a model for species accumulation curves, apparently first appeared in the palaeoecology literature (de Caprariis *et al.* 1976) and somewhat later, independently, in the entomology literature (Clench 1979).

This equation, however, enjoys a large and venerable statistical literature because it is also the Michaelis-Menten equation of enzyme kinetics. At least six different methods have been promoted by different authors for estimating S_{max} and B from a set of values for $S(n)$ as a function of n (in equivalent Michaelis-Menten notation) (Raaijmakers 1987). Four rely on least-squares linear regression on different algebraic transformations of the variables. Of these, Raaijmakers (1987) reviews all transformations and makes a strong case in favour of

$$S(n) = S_{max} - \frac{BS(n)}{n}, \tag{3}$$

known as the Eadie-Hofstee equation. This transformation assumes that $S(n)$ is a function of $S(n)/n$ (effectively, that the number of species in a sample is a function of the ratio of species to individuals in the sample).

Unfortunately, using standard linear regression in an Eadie-Hofstee plot (even for independent data points, as in standard enzyme kinetics experiments) seriously violates assumptions about the distribution of errors. Instead, Raaijmakers derives maximum likelihood estimators for S_{max} and B for the Eadie-Hofstee transformation. Let

$$X_i = \frac{S(n)}{n}, \quad \text{and} \quad Y_i = S(n), \tag{4}$$

then

$$\hat{B} = \frac{\bar{X}S_{yy} - \bar{Y}S_{xy}}{\bar{Y}S_{xx} - \bar{X}S_{xy}}, \tag{5}$$

and

$$\hat{S}_{max} = \bar{Y} + \hat{B}\bar{X}, \tag{6}$$

where S_{yy}, S_{xx}, and S_{xy} are the sums of squares and cross-products of the deviations

$$Y_i - \bar{Y} \quad \text{and} \quad X_i - \bar{X}. \tag{7}$$

Raaijmakers also provides maximum likelihood estimators for the variance of S_{max} and B. Using successive values of $S(n)$ and n to supply the

supposedly independent sample variates X_i and Y_i, however, probably makes statistical nonsense of the variance estimates.

Although the statistical propriety of the estimate for S_{max} is also questionable (as pointed out by Lamas *et al.* (1991) for the least squares model) due to non-independence, Raaijmakers' method may nonetheless be the best of the alternatives for fitting a hyperbola to data. In any case, according to Raaijmakers (1987), the double inverse regression ($1/S(n)$ on $1/n$), the Lineweaver-Burke plot (as used, for example, by Palmer (1990) in his 'Monod' model), is the worst possible transformation, producing strongly biased estimates, and thus should be avoided.

The upper set of points in figure 1 shows the maximum likelihood estimates for S_{max} corresponding to successively larger subsets of the points in the species accumulation curve for the rainforest seedling example. (Lamas *et al.* (1991) also used this approach to evaluate estimates of species richness from a species accumulation curve.) Clearly, the estimate is not as independent of n as one would wish, underestimating true richness for smaller samples sizes. The line through the points in the lower (species accumulation) curve in figure 1 plots equation (2) with parameters estimated by Raaijmakers' method for the full set of 121 points in the randomized curve. Total richness (the asymptote S_{max}) as estimated by Raaijmaker's maximum likelihood technique is 35 (34 species were actually found). For this data set, a least-squares fit to the Eadie-Hofstee equation gives the same estimate, to the nearest species.

An alternative approach to estimating the variance (and thus confidence intervals) for the asymptote of equation (2) is to estimate the asymptote S_{max} for each of a sufficiently large number of randomizations of the sample accumulation order, then compute the variance of this sample of estimates. For 25 randomizations of sample order for the seed-bank data (including all 121 samples and using Raaijmaker's maximum likelihood method), the mean is 36.8 species, with 95% confidence interval (35.9, 37.6). Note that this estimate is higher than the single estimate (35.9 species) from the mean species accumulation curve of figure 1. This approach has not been evaluated in the statistical literature (as far as we know) and is suggested in hopes that a competent statistician will accept the challenge.

Palmer (1990) reviewed two non-asymptotic models for species accumulation curves. The first is the log-linear model first proposed by Gleason (1922), in which $S(n)$ is assumed to be a linear function of the logarithm of area (a proxy for n). The second is the log–log model, in which the logarithm of $S(n)$ is assumed to be a linear function of the logarithm of area (or n); this is equivalent to the standard species–area curve of island biogeography (MacArthur & Wilson 1967). (See Stout & Vandermeer (1975) and Baltanás (1992) for an asymptotic version of this model.)

Palmer established 30 field plots, each 0.1 ha, with completely known species richness of trees and shrubs. The estimation procedures were tested using data from 40 random quadrats, each 2 m^2, placed within each plot. The species accumulation curves were produced by randomizing the order of sequential accumulation, as in the seed-bank study of figure 1. The curves were fitted to appropriately log-transformed data by linear regression, then extrapolated to the true plot size to obtain estimates of species richness. The log–log model produced extreme overestimates of true richness for Palmer's data. The log-linear model performed much better on these data, but still not as well as some of the non-parametric methods we discuss in the next section. Palmer also tested a hyperbolic model (his 'Monod' model), but used the (allegedly) badly biased Lineweaver-Burke approach (Raaijmakers 1987), as noted earlier.

With either asymptotic or non-asymptotic models for species accumulation curves, the most useful information, in practical terms, is often likely to be a prediction of the increase in richness expected for a given level of additional sampling effort or additional area sampled, rather than total local richness for a defined area. Alternatively, the amount of additional effort required to reach a given number of species or a given proportion of the total number of species present can be estimated. This approach is developed by Caprariis *et al.* (1976, 1981), Lamas *et al.* (1991), and Soberón & Llorente (1993).

The crux of the matter, however, is that extrapolation using different models for the species accumulation curve predicts different values of $S(n)$ for a given n (Palmer 1990; Soberón & Llorente 1993); by its very nature, extrapolation multiplies bias as well as case-to-case random error. Moreover, there is every reason to expect that different models may prove to be more effective for different groups of organisms or different environments, since the shape of a species accumulation curve (Miller & Wiegert 1989), like the shape of rarefaction curves (Simberloff 1979; Tipper 1979; James & Rathbun 1981) and random placement curves (Coleman 1981; Coleman *et al.* 1982) depends upon the pattern of relative abundance among species sampled.

For example, in some species accumulation curves (or some randomizations of accumulation sequences), a rapid initial increase of $S(n)$ forces the Eadie-Hoffstee transformation (equation 3) to produce an estimate of S_{max} that actually falls below $S(n)$ for large n (Lamas *et al.* 1991; Soberón & Llorente 1993). Although Lamas *et al.* (1991) suggest a procrustean solution to this problem (by forcing the curve, mathematically, to pass through the last point of the species accumulation curve), one might rather suggest that a different model be used when the hyperbolic model obviously fits so poorly.

Although Soberón & Llorente (1993) argue for the *a priori* choice of models for species accumulation curves, we believe the best approach for the present is a pragmatic one: test all reasonable models as rigorously as possible against known standards (complete or nearly complete inventories) for a wide variety of taxa and localities, while avoiding summary judgments based on single data sets (a failing of the

frenzy of papers comparing diversity indices in the 1970s). Bunge & Fitzpatrick (1993) review additional curve-fitting procedures that have been used for vocabulary estimation from literary texts, which might also be tried.

(*b*) *Fitting parametric models of relative abundance to estimate richness*

A different approach to estimating unknown species richness from samples depends directly on patterns of relative abundance, as expressed in frequency distributions of species abundances in large samples, or, equivalently, rank-abundance plots (May 1975; Pielou 1975, 1977). Although other parametric models have been proposed, the most promising models for the purpose of estimating richness from samples are the lognormal (Preston 1948), Poisson-lognormal (Bulmer 1974), and log-series (Williams 1964). A fourth distribution, the zero-truncated GIGP (generalized inverse Gaussian-Poisson) has shown promise for related problems in informetrics (such as estimating the number of unobserved non-writers of scientific articles from an observed distribution of papers per author) (Burrell & Fenton 1993), but requires daunting computations beyond our capabilities, and thus awaits evaluation elsewhere for biological data sets. (Bunge & Fitzpatrick (1993) cite a paper in press in *Ecology* by H. S. Sichel on this subject, which we have not seen.)

The data requirements for fitting parameters to these distributions are fundamentally different than for species accumulation curves. Whereas the model for species accumulation curves requires only presence–absence data for the species in samples, and allows species already discovered in an area to be ignored thereafter, data for fitting parametric models of relative abundance require counts of individuals, of both old and new species, on at least a logarithmic scale of accuracy. Collecting data adequate for fitting these distributions can add a substantial cost in time and effort for a large inventory, compared to collecting presence–absence data; thus the benefit must be clearly weighed against this cost.

The Preston (continuous) lognormal and the log-series distributions are well-known and have been thoroughly reviewed in the literature (Williams 1964; May 1975; Pielou 1975, 1977; Taylor 1978; Ludwig & Reynolds 1988; Magurran 1988). Of the two, only the lognormal actually allows direct estimation of the total number of species, by 'integration' (actually, summation of discrete categories) over the 'hidden' portion of the curve to the left of the 'veil line': the boundary between the undiscovered moiety and the singletons (species represented by only one individual).

In contrast, the log-series model assumes that the modal class is always the singletons, regardless of how large the sample becomes; thus there is no limit to the number of species in the distribution. Nonetheless, just as with non-asymptotic models for species accumulation curves, return-on-effort and effort-to-goal predictions can be made, since a log-series curve, if it fits the data well, allows quite accurate predictions of the number of new species likely to be found in larger samples. Moreover, although the log series predicts infinite numbers of species in the limit, this difficulty need not arise in practice because the number of individuals in an area is always limited. If estimates of total biomass of the target taxon and information on size classes were combined to estimate the total number of individuals in the target area, the log series model could be used to estimate total local species richness.

Fitting the continuous lognormal distribution involves a number of debatable assumptions and practices. First, the use of a continuous function to fit discrete data is problematic, especially for samples of small or moderate size. Second, the choice of the interval for abundance categories affects the estimated parameters as well as the power of the goodness of fit test. Log base 2 octaves versus log base 3 (or other) groupings yield different estimates of total richness. Third, the singleton class presents special difficulties. For example, Ludwig & Reynolds (1988) allocate half the singletons to the first (0.5–1) octave and half to the second (1–2) octave. The doubletons are then split between the second and third octaves. This treatment underestimates the 0.5–1 octave, however, because only 'whole' individuals are actually observed; most species expected to appear in fractional abundances are not seen. Thus the 1–2 octave nearly always appears, spuriously, as the modal octave, since by this procedure it must contain more species than the 0–1 octave, and quite frequently contains more species than the 2–4 octave. This bias affects the estimate of the mean. Magurran (1988) uses a broader interval for octaves with cut-points at fractional values to avoid the problem of allocating integer values, but of course the answer differs as a result.

A final problem with the continuous lognormal model is that there is no analytic solution available for the confidence interval on the estimate of the area under the curve (Pielou 1975). The importance of confidence intervals on estimates of species richness (or some other measure of reliability of the estimate) can scarcely be overemphasized. In sum, fitting the continuous lognormal to sparse samples (low individual: species ratio) is problematic for a number of reasons, and should probably be avoided.

Fitting the 'Poisson', or discrete lognormal rather than the continuous lognormal does not require the assumption that discrete numbers of individuals 'approximate' a continuous curve (Bulmer 1974). The data need not be smoothed or grouped into 'octaves', and the confidence intervals on the total species richness are obtainable in principle. Despite the tractability of the model it has been little used, probably because it is difficult to fit. Ross (1987) offers a statistical package that includes maximum likelihood fits of the Poisson lognormal. In our experience, the model tends to yield the highest estimates of any method treated here and is certainly quite different from the continuous lognormal model, a behaviour noted by Slocum *et al.* (1977). It deserves further evaluation.

(c) *Non-parametric methods for estimating species richness from samples*

In the literature of statistics, estimating the true number of classes (species or 'types') in a statistical population from a random sample of classifiable objects (individuals or 'tokens') is a classical problem with a substantial historical literature in many unrelated disciplines. Bunge & Fitzpatrick (1993) have ably reviewed and classified, by statistical criteria, the scattered literature on this problem, as applied to estimation of total number of artifact types (e.g. coin dies) based on archaeological samples, vocabulary size estimation based on literary samples, library holdings estimation from circulation data, number of undiscovered software bugs based on reported bugs, undiscovered celestial 'objects' in astronomy, unreported political executions in South Vietnam, and so on.

Applications in ecology include not only the estimation of species richness, but the estimation of population size from mark–recapture records: a formally equivalent problem, as capture probabilities vary among individuals in a population just as the relative abundance of species varies in a species assemblage. A handful of non-parametric methods have either been developed specifically for estimating species richness from samples (Heltshe & Forrester 1983; Chao 1984; Smith & van Belle 1984) have been adapted to do so from mark–recapture applications (Burnham & Overton 1978, 1979; Chao 1987), or were developed for the general class-estimation problem (Chao & Lee 1992). In terms of data requirements, most of these techniques require something intermediate between the minimum necessities for the plotting and extrapolation of species accumulation curves and the full, species-by-species relative abundance data needed to fit the lognormal or log-series distributions. All are non-parametric in the statistical sense, although performance clearly depends on the underlying empirical distribution.

Based on the work of Harris (1959), Chao (1984) derived a simple estimator (S_1^*, or 'Chao 1') of the true number of species in an assemblage based on the number of rare species in the sample,

$$S_1^* = S_{\text{obs}} + (a^2/2b), \tag{8}$$

where S_{obs} is the observed number of species in a sample, a is the number of observed species that are represented by only a single individual in that sample (i.e. the number of singletons), and b is the number of observed species represented by exactly two individuals in that sample (the number of 'doubletons'). Although Chao (1984) points out that the estimator is actually a lower bound, she found that it performed well on several test data sets, especially if most of the information in the sample is concentrated in the lower frequency classes, i.e. 'short range' frequency data with a preponderance of relatively rare species. As this is the most common situation in inventories of very diverse groups, Chao's (1984) estimator deserves serious consideration.

The estimator S_1^* relies on the distribution of individuals among species and requires data on singletons and doubletons. The same approach, however, can be applied to the distribution of species among samples, which requires only presence–absence data. In this form,

$$S_2^* = S_{\text{obs}} + (L^2/2M), \tag{9}$$

where L is the number of species that occur in only one sample ('unique' species), and M is the number of species that occur in exactly two samples. We call this estimator 'Chao 2'.

Chao (1987) developed the analogous case for the capture–recapture problem, in which trapping dates are equivalent to samples from a species assemblage (on the same or different dates), and captures of particular individuals are equivalent to occurrences of particular species in samples. Chao (1987) provided a variance estimator that applies equally to either S_1^* or S_2^*, replacing the more complex variance estimation technique presented in Chao (1984) (A. Chao, personal communication). For S_1^*

$$\text{var}\,(S_1^*) = b\left[\left(\frac{a/b}{4}\right)^4 + (a/b)^3 + \left(\frac{a/b}{2}\right)^2\right]. \tag{10}$$

The expression for var (S_2^*) is identical, but with L replacing a and M replacing b.

Burnham & Overton (1978, 1979) originated a series of jackknife estimators (up to the fifth order) for mark–recapture estimation of animal population size, which they suggested, in a brief coda (Burnham & Overton 1979), might also be applied to the problem of estimating species richness. The jackknife is a technique for reducing the bias of estimates (Miller 1964); in this case for reducing the underestimation of the true number of species in an assemblage based on the number represented in a sample. Where n is the number of samples, the first-order jackknife reduces bias of the order $1/n$, the second-order jackknife bias of the order $1/n^2$, etc.

The first-order jackknife estimate of species richness, S_3^*, is based on the number of species that occur in only one sample (L),

$$S_3^* = S_{\text{obs}} + L\left(\frac{n-1}{n}\right), \tag{11}$$

where n is the number of samples. Heltshe & Forrester (1983) independently redeveloped the first-order jackknife, explored its usefulness for estimating species richness with extensive simulations, and derived an exact expression for the variance

$$\text{var}\,(S_3^*) = \frac{n-1}{n}\left(\sum_0^{S_{\text{obs}}} j^2 f_j - \frac{L^2}{n}\right), \tag{12}$$

where f_j is the number of samples containing exactly j of the L unique species. Karr *et al.* (1990) used the first-order jackknife to compare the species richness of birds in four neotropical rainforests, based on a series of 100-capture mist net records at each site.

Burnham & Overton's (1978, 1979) second-order jackknife estimate, S_4^* (like the Chao 2 estimator) is based on the number of species that occur in only one

sample (L), as well as the number that occur in exactly two samples (M):

$$S_4^* = S_{\text{obs}} + \left[\frac{L(2n-3)}{n} - \frac{M(n-2)^2}{n(n-1)}\right]. \quad (13)$$

Smith & van Belle (1984) independently re-derived this estimator (which unfortunately appears with a typographical error in their paper; see Palmer 1991), and explored its properties and behaviour under various assumptions. The variance can be estimated (Burnham & Overton 1978; and references in Smith & van Belle 1984).

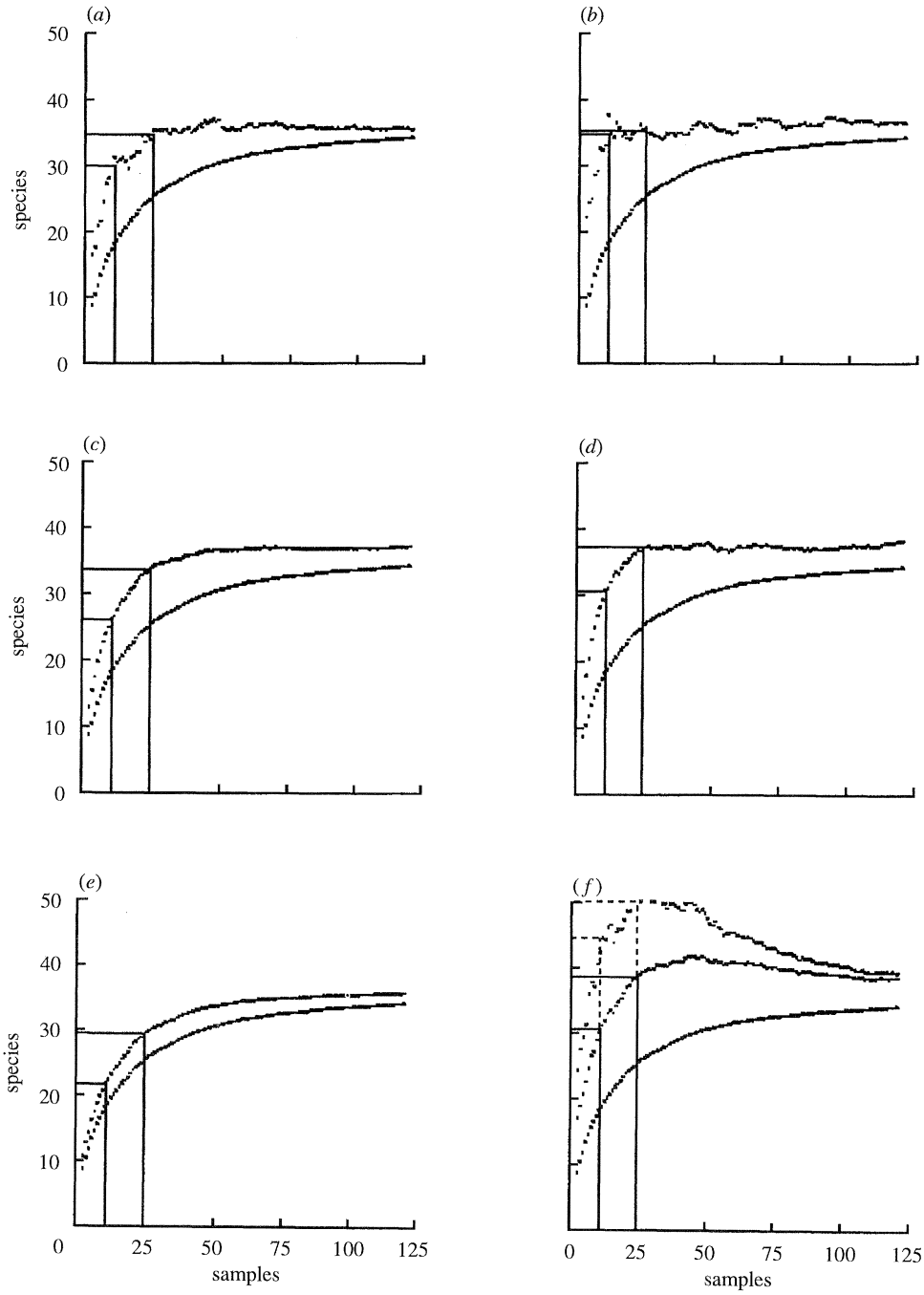

Figure 2. Performance of seven non-parametric estimators of species richness for an empirical data set. (*a*) S_1^*, Chao 1; (*b*) S_2^*, Chao 2; (*c*) S_3^*, Jackknife 1; (*d*) S_4^*, Jackknife 2; (*e*) S_5^*, Bootstrap; (*f*) S_6^* & S_7^*, Chao & Lee 1 & 2. The lower curve in each panel (the species accumulation curve) plots the observed number of species as a function of the number of pooled samples for the rainforest seed-bank study outlined in the text. The upper curve(s) in each panel displays the estimated total species richness based on successively larger numbers of samples from the data set. The species accumulation curve itself is a strongly (negatively) biased estimator of species richness. The seven methods reduce this bias (or reverse it, in the case of the Chao and Lee estimators) to different degrees; for each estimator, the estimates based on 12 and 25 samples are indicated by coordinate 'boxes' to allow visual comparison of the estimates based on small numbers of samples (see table 2). For this data set, Chao 2 (*b*) provides the least biased estimates of species richness for small numbers of samples, with Jackknife 2 (*d*) a close second. For all curves, each point is the mean of 100 estimates based on 100 randomizations of sample accumulation order.

Table 1. *Estimated total species richness based on 12, 25 and 121 samples from the seed-bank study discussed in the text, for eight estimators (from unpublished data provided by B. Butler and R. L. Chazdon; see also figures 1 and 2). Each value represents the mean for 100 randomizations of sample order*

	number of samples		
species richness estimator	12	25	121
S_{obs}	18.6	25.2	34.0
individuals	94.8	197.5	952.0
S_1^* Chao 1	30.0	34.8	35.0
S_2^* Chao 2	34.6	35.5	36.3
S_3^* Jackknife 1	26.5	33.6	37.0
S_4^* Jackknife 2	30.8	36.8	38.0
S_5^* Bootstrap	22.1	29.2	35.6
S_6^* Chao & Lee 1	30.9	38.6	38.4
S_7^* Chao & Lee 2	44.4	50.2	39.2
Michaelis-Menten	26.9	29.8	35.9

Smith & van Belle (1984) also derived a bootstrap estimate of species richness, based on p_j, the proportion of quadrats containing each species j,

$$S_5^* = S_{obs} + \sum_{j=1}^{S_{obs}} (1 - p_j)^n. \quad (14)$$

They provide a complicated expression for variance estimation.

Palmer (1990, 1991), in the forest vegetation study discussed previously, evaluated the first- and second-order jackknife and the bootstrap estimators (S_3^*–S_5^*). He found all three to be useful estimators, but overall the jackknife estimators, S_3^* and S_4^*, performed better than the bootstap, for Palmer's data sets, a finding we later confirm for the seed-bank example.

Chao & Lee (1992) developed two, closely related estimators based on sample 'coverage' (the sum of the parametric relative abundance probabilities of the observed species) that take into account the pattern of relative abundance of species in samples, and thus require full relative abundance data. We will refer to these estimators as S_6^* and S_7^* (Chao & Lee 1 & 2). The two estimators differ only in the way the coefficient of variation of the empirical data is estimated. Although these estimators performed well in Chao & Lee's simulation studies using a spectrum of negative binomial distributions, and Bunge & Fitzpatrick (1993) concluded that the approach was especially promising, our results for the seed-bank data are so poor (figure 2) that we will not present the rather complex equations here. Nonetheless, further developments in the area of coverage estimation bear watching.

In figure 2 and table 1, we present a comparative study of the behaviour of richness estimators S_1^*–S_7^* (equations 8, 9, 11, 13 and 14, and Chao & Lee's (1992) coverage-based estimators), for the rainforest seed-bank study of Butler & Chazdon (unpublished data), outlined in a previous section. (Table 1 also includes results for the Michaelis-Menten approach, for comparison.) The strategy in figure 2, as in figure 1, is to see how well each estimator approximates true richness based on successively larger numbers of accumulated samples. The 'coordinate boxes' in figure 2 show the estimated richness for 12 samples (the point at which the observed richness – the species accumulation curve – reaches approximately half (18 species) the true richness (34 species observed)) and for 25 samples (details appear in table 1).

All the estimators provide adequate bias reduction for large samples (e.g. more than about 50 accumulated samples), except for the Chao and Lee estimators, which have a large positive bias. It is small samples, however, that are of the greatest interest for richness estimation; a curve that has reached an obvious asymptote requires no statistics. For this data set, the Chao 2 and second-order Jackknife estimators clearly provide the least biased estimates for small numbers of samples, followed by the first-order jackknife and the Michaelis-Menten method. In fact the Chao 2 estimator, which requires only presence–absence data, provides a remarkably accurate estimate (34.6) of true species richness (34 species observed), based on as few as 12 samples, including less than 100 individuals of 18 species.

A full evaluation of all these methods awaits trial by fire with real data sets for a diverse range of organisms and habitats (see Palmer 1990, 1991), as well as thorough exploration with simulated data sets (see Heltshe & Forrester 1983; Chao & Lee 1992; Baltanás 1992). As figure 2 shows, however, all these non-parametric estimators must underestimate the true richness if the sample is too sparse. For example, if the sample contained just one doubleton and the rest singletons, the Chao 1 estimator S_1^* would attain its maximum value of $(S_{obs}^2 + 1)/2$. The Chao 2 estimator S_2^* attains a similar maximum if one species occurs in two samples and the remainder in one. The jackknife and bootstrap estimates S_3^*, S_4^* and S_5^* attain their maximum values of approximately twice S_{obs} if all species are 'uniques', each found in just one sample. In practical terms, the jackknife estimates have upper bounds of about double, and Chao's estimators about half the square of the observed number of species. Therefore, these estimators should correlate strongly with sample size until half (or the square root of twice) the total fauna is observed and thereafter become gradually independent of sample size until finally the observed richness and the estimate converge.

Indeed, one can ask under what circumstances S^* converges on S_{obs}. For any of the estimators that are based on replicate samples, $S_{obs} = S^*$ when every species occurs in at least two samples (S_2^*,S_3^*,S_4^*). For estimators, such as S_1^*, that pay attention to relative abundance, $S_{obs} = S^*$ when all species are present in abundances of two or greater. Both of these 'stop rules' are intuitively sensible: the first states that the census is complete if all species are observed 'multiple' times during the work. The second states that the census is complete if all species are 'not rare'. Of course, the precise meaning of 'multiple' or 'not rare' is debatable, but either approach seems heuristically sound.

5. COMPLEMENTARITY

(*a*) *Measures of complementarity*

We return now to the concept of complementarity, or

biotic distinctness, outlined in the Introduction. Scores of measures of similarity and difference exist in the literature of statistical ecology, biogeography, ordination, and phenetics that have been or could be applied to contrasting biotas (see Cheetham & Hazel 1969; Pielou 1984; Ludwig & Reynolds 1988). We present here the simplest measure we have found that captures the meaning of the complementarity of two biotas, yet has a respectable statistical pedigree: the proportion of all species in two sites that occurs in only one or the other of them.

Suppose we compare accurate species lists for two sites, and find that the first site has a local richness of S_j species while the second has S_k species. If the number of species in common between the two lists is V_{jk}, then the total richness for both sites combined is

$$S_{jk} = S_j + S_k - V_{jk}, \tag{15}$$

and the number of species unique to either list (equivalently, the number of 'mismatches' between the two lists) is

$$U_{jk} = S_j + S_k - 2V_{jk}. \tag{16}$$

Then the complementarity of the two lists is just

$$C_{jk} = \frac{U_{jk}}{S_{jk}}. \tag{17}$$

Thus complementarity, as measured by C, varies from zero (when the lists are identical) to unity (when the lists are completely distinct); or from 0 to 100%, if expressed as the percentage of species that are complementary. For computation from presence–absence matrices, a useful re-formulation is

$$C_{jk} = \frac{\sum_{i=1}^{S_{jk}} |X_{ij} - X_{ik}|}{\sum_{i=1}^{S_{jk}} \max(X_{ij}, X_{ik})}, \tag{18}$$

where X_{ij} and X_{ik} are the presence–absence (1,0) values for species i in list j and list k.

In the literature of statistical ecology, the measure C is known is the Marczewski-Steinhaus (M-S) distance (Holgate 1969; Pielou 1984). The complement of the more familiar Jaccard index of similarity, the M-S distance is a true metric, having been shown to satisfy the triangle inequality (Levandowsky & Winter 1971).

When more than two species lists are compared, U_{jk} may be computed for adjacent pairs of points along a gradient, or for all possible pairs of lists in a mosaic environment. If S_T is the total number of species in the combined grand list for all local lists pooled, using S_T in the denominator for sets of pairwise comparisons makes the 'units' of distance equivalent for all comparisons within a set of sites, if desired (see Pielou 1984, pp. 60–61; Orloci 1978). As an overall measure of complementarity (heterogeneity) for a set of lists, E. C. Pielou (personal communication) has suggested computing

$$C_T = \frac{\sum U_{jk}}{n}, \tag{19}$$

where n is the number of samples, and the summation is over all pairs of samples; C_T reaches a maximum value of $nS_T/4$, for sufficiently large n.

(*b*) *Some examples of differing complementarity*

In tables 2, 3, and 4, we present some examples of complementarity (distinctness) patterns for neotropical faunas, using C_{jk} (equation 17) expressed as a percentage. Table 2 extends the example of hummingbird biogeography presented from the Introduction. In addition to the comparisons between sites at decreasing elevations in Costa Rica (Cerro de la Muerte at 3100 m, Monteverde at 1400 m, and La Selva in the Atlantic lowlands), the table includes data from three additional lowland rainforest sites with high hummingbird richness (Karr *et al.* 1990) in Panama (Barro Colorado Island and Pipeline Road), Peru (Cocha Cashu Biological Station in Manu National Park) and Brazil (the Biological Dynamics of Forest Fragments Project reserves near Manaus) (Gentry 1990).

The matrix of complementarity values shows a moderate level of distinctness between the hummingbird faunas of La Selva and Barro Colorado (only 61% distinct; about 500 km apart), whereas the two South American sites are more complementary (79%

Table 2. *Richness and percentage complementarity of hummingbird faunas among three elevations in Costa Rica and four neotropical lowland rainforests (data from Colwell 1973, Feinsinger 1976, Karr* et al. 1990)

(Matrix entries: percentage complementarity (number of species in common).)

	Cerro de la Muerte, Costa Rica	Monteverde, Costa Rica	La Selva, Costa Rica	Barro Colorado, Panama	Manaus, Brazil	Manu, Peru
elevation/m	3100	1400	100	50	100	300
richness	5	14	25	21	11	18
complementarity:						
Monteverde	88 (2)					
La Selva	100 (0)	85 (5)				
Barro Colorado	100 (0)	91 (0)	61 (13)			
Manaus	100 (0)	100 (0)	94 (2)	93 (2)		
Manu	100 (0)	100 (0)	90 (4)	82 (6)	79 (5)	

Table 3. *Richness and percentage complementarity of spider faunas along an elevational gradient in Bolivia (Coddington* et al. *1991; J. A. Coddington & L. H. Young, unpublished data)*

(Sequential sites are separated by about 110 km Matrix entries: percentage complementarity (number of species in common).)

	El Trapiche	Río Tigre	Cerro Uchumachi
elevation/m	100	500	1900
richness	191	329	158
complementarity:			
Rio Tigre	97 (15)		
C. Uchumachi	99 (2)	99 (4)	

distinct; 1500 km apart). Strikingly, the level of complementarity between adjacent elevations within Costa Rica (85 and 88%, even though less than 100 km apart), however, is nearly as great as between La Selva and Manaus (94%) or La Selva and Manu (90%; each site about 3000 km from La Selva).

Recently gathered data on the diversity of spiders along an altitudinal transect between three stations at 100 m, 500 m, and 1900 m in Bolivia (Coddington *et al.* 1991; J. A. Coddington & L. H. Young, unpublished data) show quite a different pattern of complementarity (table 3) than the hummingbird data (table 2), although comparisons must be tentative owing to differences in completeness of the inventories (see next section). Richness does not vary as dramatically with elevation in the spider study, and the mid-elevation site was more diverse (329 species observed) than the lowland site (191 species), which was in turn more diverse than the highest site (158 species). Very few spider species (less than 3%) were shared between any of the Bolivian sites, and none were common to all three, even though the sites were separated by less than 120 km. Overlap of any of these faunas with Peruvian faunas, only a few hundred kilometres north, is virtually nil.

The degree of faunal complementarity for spiders is just as striking on a very local scale, as shown in a similar study in Manu National Park in Peru (table 4)

Table 4. *Richness and percentage complementarity of spider faunas among contiguous, similar forest types within the floodplain of the Manu River, Peru (Silva & Coddington 1994)*

(Matrix entries: percentage complementarity (number of species in common).)

	old alluvial terrace	upper floodplain forest	dissected alluvial terrace
richness	324	250	107
complementarity:			
upper floodplain forest	64 (152)		
dissected alluvial terrace	81 (70)	85 (57)	

(Silva & Coddington 1994). Within the floodplain of the Manu River, several distinct forest types can be recognized, including upper floodplain forest, old alluvial terraces, and dissected alluvial terraces. Sampling from these three forest types in a local habitat mosaic yielded complementarities ranging from 64% to 82%; about the same as for hummingbirds between Manu and Manaus, 3000 km distant. Although perhaps exaggerated in this comparison due to incomplete inventories in the spider studies, geographic distributions of terrestrial invertebrates tend to be patchier, more seasonal, have more species with smaller ranges, and be subject to wider fluctuations in abundance (e.g. Wolda 1978) than distributions of terrestrial vertebrates.

(*c*) *Complementarity of samples*

So far, in this discussion of complementarity, we have assumed that species lists are known with certainty. In fact, for hyperdiverse taxa (and initially all taxa in a poorly known region) they will most assuredly be subject to sampling error. (For example, compared to the hummingbird data, above, the spider data are far more approximate.) Samples of insufficient size ('undersampling') consistently underestimate local richness, but the effect of undersampling on estimates of complementarity are more complex.

First, note that undersampling consistently underestimates geographical range, ecological range (e.g. host range for a parasite or herbivorous arthropod), phenological scope (e.g. flowering period or emergence period), or any other variable estimated from discrete points in time or space. Qualitatively, this effect does not depend upon the true distribution of individuals or events in time or space (Colwell & Hurtt 1994); range is correlated with sample size even for a uniform distribution. Quantitatively, the shape of the true distribution affects the rate at which range increases with sample size.

Geographic or ecological ranges estimated by sampling points along a species richness gradient or among the phases of a mosaic that differ markedly in species richness are subject to an additional problem. If samples are standardized by using equal-sized quadrats, equal number of stems, equal numbers of trap or net hours, equal volumes of soil or sediment, or equal observation times or any other measure of equal sampling effort or sample size, the severity of range underestimation will tend to be directly correlated with richness. This occurs because the sample size, per species, tends to be smaller in richer samples when equal numbers of individuals have been sampled or equal effort has been expended. If severe enough, this effect may lead to an inflated or even spurious 'Rapoport effect', a negative correlation among sampling points between mean range size of the species sampled and their local richness (Colwell & Hurtt 1994). Unless all samples are sufficiently large to overcome this effect, the best antidote is to adjust the size of samples in proportion to the estimated richness of each point, ideally such that average

number of individuals per species is approximately equivalent. Even so, rarer species will always have their ranges more severely underestimated than common species.

In general, the complementarity (distinctness) of two (or more) samples will be overestimated under the same conditions that ranges are underestimated, because an undersampled species will tend to occur in fewer samples than it should, especially at the edge of its range, assuming a modal distribution. (The exception might be comparisons between high-dominance communities in which the common species are widespread and rare ones tend to be locally endemic. In this case, two small samples might underestimate complementarity by yielding the same few common species, missing many rare species that would differentiate the sites in a larger sample.) For the same reasons, complementarity will generally be more severely overestimated between samples of higher richness than between species-poor samples, unless sample size is compensatorily increased for high-richness samples, or all samples are sufficiently large.

The quantitative integration of richness and complementarity presents an important but poorly studied challenge. May (1990) outlined one possible approach, by developing a way to compute the 'effective specialization' of species among resource states or samples (tree species, in his example), reckoning richness estimates as weighted sums of species contributions. May stresses, however, that sampling effects must somehow be separated from biological ones to make headway with this approach. When relative abundance data are available, rather than simply species lists, it should be possible to develop statistically sound approaches to estimating complementarity from sampling data. Grassle & Smith (1976), for example, developed a family of similarity measures based on the expected number of species shared between two samples of m individuals each, assuming multinomial distributions with differing species composition and relative abundance. Much more work needs to be done in this relatively neglected area.

6. USING RATIOS TO ESTIMATE AND EXTRAPOLATE

In the previous sections, we have taken a look at methods for estimating species richness within homogeneous habitats (or more realistically, within relatively fine-grained habitat mosaics), and we have pointed out the importance and outlined the difficulties of assessing the complementarity of species assemblages between different habitats or different localities. We now turn to a series of completely different methods for estimating species richness for poorly known taxonomic groups or localities. All these methods rely on ratios between known values of species richness to permit the estimation of unknown values (treated at length by Hammond, this volume). The accuracy of all these methods depends upon the assumption – often a tenuous one – that the relevant ratios are approximately constant among the entities compared.

(*a*) *Reference and comparison*

Virtually all ratio methods of richness estimation rely, at least implicitly, on the designation of certain localities as 'reference' sites, at which collection or census methods are calibrated, 'indicator' taxa designated, or taxon ratios established, based on a supposedly known universe of species for one or more taxa. Then, at other sites, which we will call 'comparative' sites, the denominator (say) of some ratio is measured, and its numerator solved for, using a 'calibrated' value of the same ratio established at one or more reference sites. Reference sites range from a single tree species in Panama (Erwin & Scott 1980; Erwin 1982), to a large study area in N. Sulawesi, Indonesia (Hodkinson & Casson 1991; Hammond 1992; Stork 1994), to the British Isles (Hawksworth 1991). Although, at present, the preferred comparative site is the entire Earth (e.g. Erwin 1982; Hodkinson & Casson 1991; Hammond 1992; May 1988, 1990, 1992; Stork 1994), the same approach can be used in a number of more restricted, and thus perhaps more accurate ways to help build a detailed picture of global biodiversity (as advocated by Hammond (1992)).

On the scale of biomes, proposals are afoot to establish (formally or informally) a network of reference (or 'intensive') and comparative (or 'extensive') sites around the world, with a small number of intensively studied reference sites and a larger number of comparative sites in each major biome (Solbrig 1991; di Castri *et al.* 1992*a*,*b*; Vernhes & Younès 1993; Janzen & Hallwachs 1993; Yoon 1993). On a regional scale, within any large, heterogeneous site, such as the 50 000 ha elevational transect envisioned for a tropical 'All Taxa Biodiversity Inventory' (Janzen & Hallwachs 1993; Yoon 1993), the use of reference and comparative 'sub-sites' would help make the most of available economic and human resources, especially for hyperdiverse taxa.

For example, the true species richness ratio between a relatively easily censused taxon, such as trees, and a more difficult taxon, say leaf beetles, may vary over an elevational transect. If the ratio beetles : trees is accurately assessed at, say, four elevations spanning the gradient (reference sub-sites), but only tree species data is available for stands at an additional 20 elevations along the gradient (comparative sub-sites, for leaf beetles), the local richness of leaf beetle species may be estimated for the 20 comparative sub-sites by interpolating between beetle : tree ratios at the four reference sub-sites, and multiplying by the local tree species richness at each comparative sub-site. Estimating the complementarity of the leaf beetle fauna along the gradient, based on levels of complementarity between the reference sub-sites, is more difficult, but should also be tractable.

(*b*) *Taxon ratios*

The leaf beetle : tree ratio example, above, is just of one many ways of using taxon ratios to estimate unknown patterns of biodiversity. Two general categories of taxon ratios are worth distin-

guishing: hierarchical and non-hierarchical. The leaf beetle : tree ratio is an example of the latter, as neither taxon contains the other. Non-hierarchical ratios make the most sense when there is some functional, ecological reason to suppose that such a ratio might be roughly constant or at least follow some consistent pattern (Gaston 1992). Examples of such ratios might include the ratio of herbivorous arthropods of particular taxa (Erwin 1982; Thomas 1990; Bassett 1992; Gaston 1993) or of plant-associated fungi (Hawksworth 1991) to their host plants, the ratio of predator taxa to prey taxa (Arnold 1972), or the ratios among feeding guilds (Stork 1991). Unfortunately, the approximate constancy of such ratios, at present, is in most cases more a matter of convenient supposition than of empirical evidence (Gaston 1992; Prendergast *et al.* 1993). To make the most of them as estimators, we need much additional geographically comparable data on ecologically meaningful richness ratios. A network of reference sites around the world would be an excellent way to begin. Again, not simply raw ratios, but a careful study at reference sites of the patterns of complementarity of herbivores on their hosts, predators on their prey, and so on, would be required to allow accurate estimation at comparative sites using such ratios (Stork 1988; May 1990).

Hierarchical taxon ratios, often combined with other ratios, have been used repeatedly to estimate the global richness of insects: one of the great unknowns for terrestrial biodiversity. For example, Hodkinson & Casson (1991) determined that only 37.5% of the 1690 Hemiptera species in their rainforest samples from Sulawesi, Indonesia, are described. Knowing the approximate number of Hemiptera species described for the world fauna (about 71 000) they assumed that these, too, represent 37.5% of a global total that must thus represent some 189 000 hemipteran species. Finally, given that Hemiptera currently represent about 7.5% of the described insects of the world, they assume that the same is true for the undescribed insects of the world, and use this proportion to arrive at an estimate of about 2.5 million species for the world insect fauna. In this example, Sulawesi is used was a reference site to measure the ratio of described to undescribed Hemiptera, which was then projected up the Linnean hierarchy (and around the earth) to estimate the number of undescribed species of Insecta. The appearance of 'step-by-step' estimation in such examples is illusory. In fact, the estimate depends entirely on the degree to which the state of taxonomic knowledge of Sulawesi Hemiptera is typical of global Insecta; the global estimate of 2.5 million species is simply the number of described insect species divided by 0.375.

Hierarchical taxon ratios may also be used, with perhaps less onerous assumptions, to estimate local species richness and faunal or floral composition. For example, the Arthropods of La Selva (ALAS) inventory in Costa Rica (Longino 1994) is designed to measure the richness of a series of 'focal' (reference) taxa, both by a series of standardized, mass-sampling techniques and by intensive, specialized collecting techniques. Taken together, these techniques are intended to yield virtually complete inventories for the focal taxa.

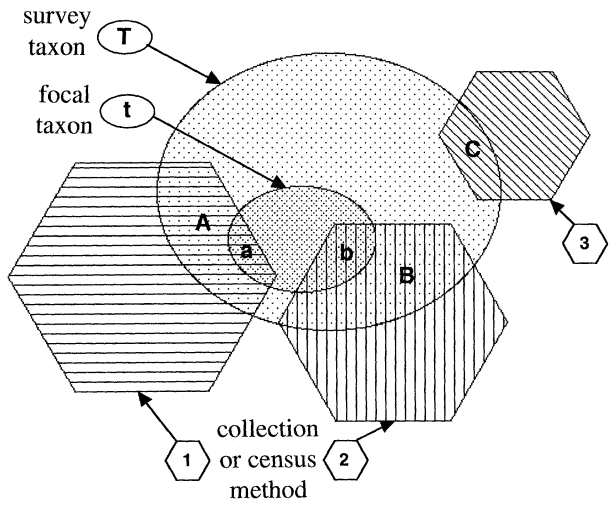

Figure 3. The use of hierarchical taxon ratios and calibrated sampling methods to estimate species richness. The objective is to estimate the richness of survey taxon **T** at a study site, given a full inventory of focal taxon **t** (a sub-taxon of **T**). Sampling method 1 reveals subset **A** of **T** and subset **a** of **t**. The richness of **T** is then estimated from the assumption that **A**/**a** approximates **T**/**t**. Analogous estimates arise from additional sampling methods 2, 3, etc. (Method 3 is uninformative in this example, as it yields no specimens of the focal taxon.) Finally, these estimates may be averaged to help eliminate the inherent biases of individual methods.

Simultaneously, the richness of a matched series of broader 'survey' taxa, each containing one of the focal taxa, is assessed by the standardized mass-sampling techniques only. For example, the weevils, family Curculionidae, are a survey taxon containing the focal taxon subfamily Zygopinae. Each of the mass-sampling methods (malaise traps, canopy fogging, black lights, Berlese samples, etc.) is 'calibrated' for each focal taxon (figure 3) by assessing the proportion of the true fauna for each focal taxon that is captured by each quantitative method. This taxon-by-method matrix of hierarchical taxon ratios can then be used to estimate the proportion of each survey taxon that has been captured and thus obtain approximate values for the true local richness of each survey taxon at the site.

This method assumes that members of a survey taxon that do not belong to the focal taxon (e.g. non-zygopine weevils) respond in approximately the same way to the quantitative collection techniques as members of the corresponding focal taxon (e.g. zygopine weevils). Averaging across several methods (figure 3) may help balance the inevitable violations of this assumption. Unlike many of the assumptions underlying global projections based on hierarchical taxon ratios, the assumption of consistent capture ratios between can be tested with a reasonable amount of effort by completing local inventories of survey taxa. Obviously, this assumption is most likely to be true within biologically conservative clades and most likely to be needed in very diverse and taxonomically difficult groups.

Meanwhile, the analysis of existing biogeographic data for well-known groups and sites (e.g. Gentry 1990; Prendergast *et al.* 1993; Hespenheide 1993) is a useful way to explore the feasibility of using taxon ratios for the

rapid assessment of species richness and faunal or floral composition. In the long run, however, only carefully designed and coordinated studies focused at the regional level on the poorly known taxa and poorly known habitats of the earth will provide an adequate understanding of global biodiversity. The magnitude of this challenge makes it well worthwhile to develop and test all reasonable methods of estimation and extrapolation as tools for the task.

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