For Jerry

Measuring Biological Diversity

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Contents

Preface vii

Chapter 1 Introduction: measurement of (biological) diversity 1
What has changed in the last 15 years? 4
Biodiversity, biological diversity, and ecological diversity 6
What this book is about . . . 9
. . . and what it is not about 10
Assumptions of biodiversity measurement 11
Spatial scale and biodiversity measurement 12
Plan of the book 15
Summary 17

Chapter 2 The commonness, and rarity, of species 18
Methods of plotting species abundance data 21
Species abundance models 27
Statistical models 28
Goodness of fit tests 43
Biological (or theoretical) models 45
Other approaches 58
Fitting niche apportionment models to empirical data 61
General recommendations on investigating patterns of species abundance 64
Rarity 66
Summary 71

chapter two

The commonness, and rarity, of species[1]

In no environment, whether tropical or temperate, terrestrial or aquatic, are all species equally common. Instead, it is universally the case that some are very abundant, others only moderately common, and the remainder—often the majority—rare. This pattern is repeated across taxonomic groups (Figure 2.1). Indeed, the adoption, by early phytogeographers such as Tansley, of characteristic species to classify plant associations (Harper 1982), implicitly recognizes that certain members of an assemblage, by virtue of their abundance, help define its identity.

Many people, as Chapter 1 observed, treat biological diversity, or biodiversity, as synonymous with species richness. However, the fact that species abundances differ means that the additional dimension of **evenness** can be used to help define and discriminate ecological communities (Figure 2.2). Evenness[2] is simply a measure of how similar species are in their abundances. Thus, an assemblage in which most species are equally abundant is one that has high evenness. The obverse of evenness is **dominance**, which, as the name implies, is the extent to which one or a few species dominate the community. It is conventional to equate high diversity with high evenness (equivalent to low dominance) and a variety of measures have been devised to encapsulate these concepts (see Chapter 4 for details).

The observation that species vary in abundance also prompted the development of species abundance models. Motomura's (1932) geometric

1 After Preston (1948).

2 Lloyd and Ghelardi (1964) introduced the term "equitability" to mean the degree to which the relative abundance distribution approaches the broken stick distribution. It is not a synonym for evenness. Cotgreave and Harvey (1994) point out that the usual meaning of equitability is "resonableness."

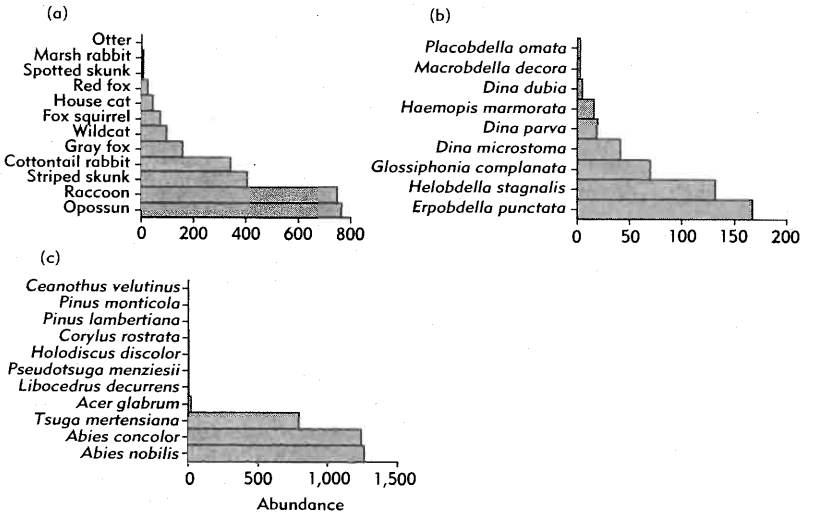

Figure 2.1 Variation in the relative abundance of species in three natural assemblages. (a) Relative abundance of larger mammals in 11 counties of southwestern Georgia and northwestern Florida (from table 1, McKeever 1959). A total of 2,688 individuals were collected during 31,145 trap nights. (b) Relative abundance (number of individuals) of leeches collected from 87 lotic habitats in Colorado (from table 1, Herrmann 1970). (c) Relative abundance of trees and shrubs found between 1,680 and 1,920 m in the central Siskiyou Mountains in Oregon and California. Abundance represents the number of stems (≥1 cm diameter) in 5 ha. (Data from table 12, Whittaker 1960.)

series and Fisher's (Fisher *et al.* 1943) logarithmic series represented the first attempts to mathematically describe the relationship between the number of species and the number of individuals in those species. Since then a variety of distributions have been devised or borrowed from other sources. Some of these models (discussed in detail below) are more successful than others at describing species abundance distributions, but none are universally applicable to all ecological assemblages. This is because both species richness, and the degree of inequality in species abundances, vary amongst assemblages. In some cases one or two species dominate, with the remainder being infrequent or rare. In other situations species abundances are rather more equal, though never totally uniform. A further complication arises from the fact that sampling may provide an incomplete picture of the underlying species abundance distribution in the assemblage under investigation (see discussion below and in Chapter 4). Yet, even with these constraints, species abundance distributions have the power to shed light on the processes that determine the biological diversity of an assemblage. This stems from the assumption that the abundance of a species, to some extent at least,

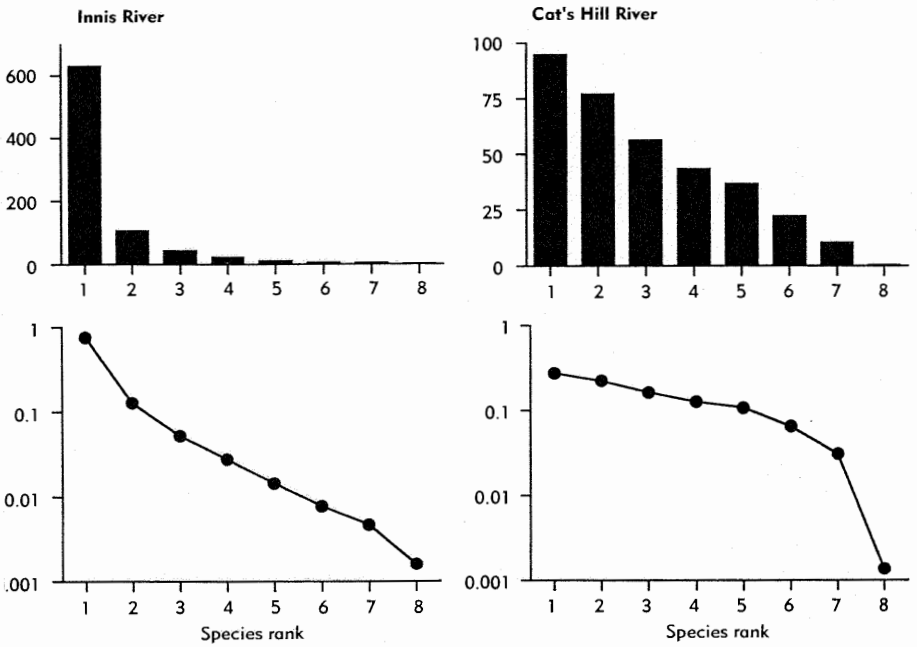

Figure 2.2 A survey of fish diversity in Trinidad revealed two assemblages with equal species richness but different evenness. (a) The abundance of the eight species of fish in the Innis River and Cat's Hill River in Trinidad is shown using a linear scale. (b) The same data are expressed as relative abundance and presented in the form of a rank/abundance plot. Note the logarithmic scale. The greater evenness of the Cat's Hill River assemblage is evident from the shallower slope in the rank/abundance plot. In this assemblage the most dominant species (*Astyanax bimaculatus*) comprised 28% of the total catch. This contrasts with the less even Innis River in which the most dominant species (*Hypostomus robinii*) represented 76% of the sample. (Data from study described by Phillip 1998.)

reflects its success at competing for limited resources (Figure 2.3). No assemblage has infinite resources. Rather, there are always one or more factors that set the upper limit to the number of individuals, and ultimately species, that can be supported. Classic examples of limited resources are the light reaching the floor of a tropical rain forest (Bazzaz & Pickett 1980), nutrients in the soil (Grime 1973, 1979), and the space available for sessile organisms on rocky shores (Connell 1961). (The relationship between productivity and patterns of abundance can be complex—a point well articulated elsewhere (Huston 1994; Rosenzweig 1995; Gaston & Blackburn 2000; Godfray & Lawton 2001).) In one of the most comprehensive reviews of the subject to date, Tokeshi (1993) strongly advocates the study of species abundance relationships. He argues that

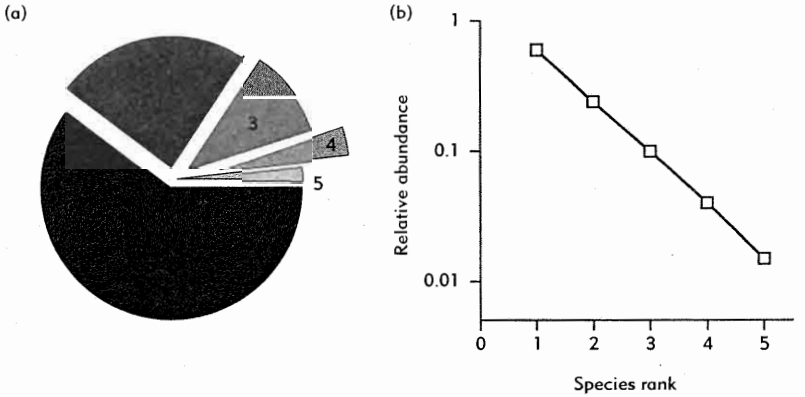

Figure 2.3 The relationship between niche apportionment and relative abundance. (a) Niche space (represented as a pie diagram) being successively carved up by five species each of which takes 0.6 of the remaining resources. Thus, species 1 pre-empts 0.6 of all resources, species 2 takes 0.6 of what is left (i.e., 0.6 of the remaining 0.4 which equals 0.24) and so on until all have been accommodated. (b) An illustration of the assumption that this niche apportionment is reflected in the relative abundances of the five species. This outcome is consistent with the geometric series when $k = 0.6$.

if biodiversity is accepted as something worth studying (Chapter 1), it follows that species abundance patterns deserve equal and possibly even greater attention. The goal of this chapter is to review the models proposed to account for the distribution of species abundances in ecological assemblages. It provides guidelines on the presentation and analysis of species abundance data and concludes by discussing the concept of rarity in the context of species abundance distributions. Some (though not all) of the methods assume that abundance comes in discrete units called individuals. In other cases abundance is assumed to be continuous (biomass is an example). I touch on these matters as they arise and explore the issue of different types of abundance measure further in Chapter 5.

Methods of plotting species abundance data

Comparative studies of diversity are often impeded by the variety of methods used to display species abundance data. Different investigators have visualized the species abundance distribution in different ways. One of the best known and most informative methods is the **rank/abundance plot** or **dominance/diversity curve** (Figure 2.4). In this species are plotted in sequence from most to least abundant along the horizontal (or x) axis. Their abundances are typically displayed in a $\log_{10}$ format (on the y axis)—so that species whose abundances span several orders of magni-

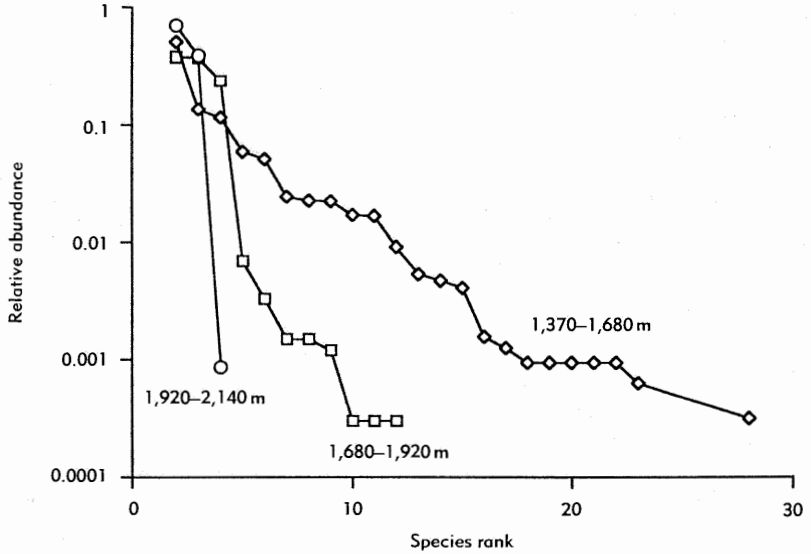

Figure 2.4 An example of a rank/abundance or Whittaker plot. The *y* axis shows the relative abundance of species (plotted using a $\log_{10}$ scale) while the *x* axis ranks each species in order from most to least abundant. The three lines show the densities of trees, in relation to elevation, on quartz diorite in the central Siskiyou Mountains in California and Oregon. Species richness decreases, and assemblages become less even (as indicated by increasingly steeper slopes) at higher altitudes. (Data from table 12, Whittaker 1960.)

tude can be easily accommodated on the same graph. In addition, and in order to facilitate comparison between different data sets or assemblages, proportional or percentage abundances are often used. This simply means that the abundance of all species together is designated as 1.0 or 100% and that the relative abundance of the each species is given as a proportion or percentage of the total. Krebs (1999) recommends that these plots be termed **Whittaker plots** in celebration of their inventor (Whittaker 1965).

One advantage of a rank/abundance plot is that contrasting patterns of species richness are clearly displayed. Another is that when there are relatively few species all the information concerning their relative abundances is clearly visible, whereas it would be inefficiently displayed in a histogram format (Wilson 1991). Furthermore, rank/abundance plots highlight differences in evenness amongst assemblages (Nee *et al.* 1992; Tokeshi 1993; Smith & Wilson 1996) (Figure 2.5). However, if *S* (the number of species) is moderately large the logarithmic transformation of proportional abundances can have the effect of de-emphasizing differences in evenness. Rank/abundance plots are a particularly effective method of

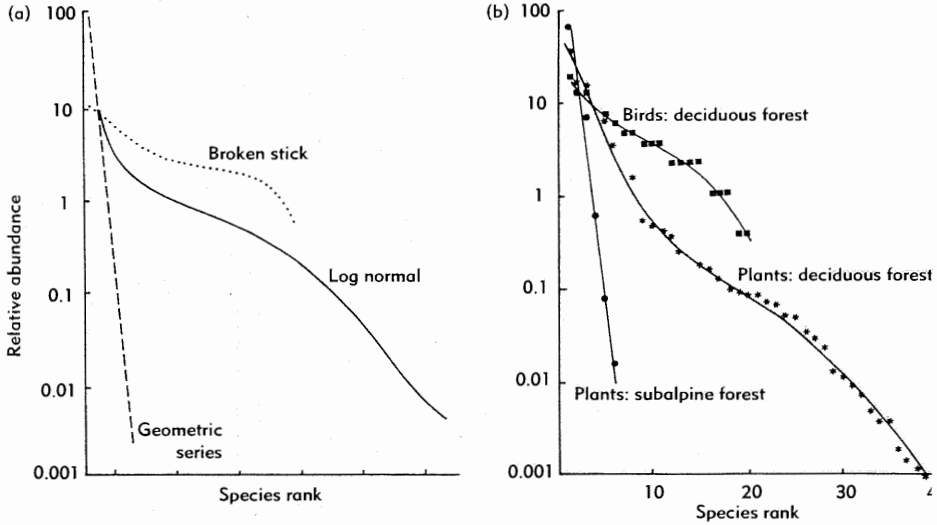

Figure 2.5 (a) Rank/abundance plots illustrating the typical shape of three well-known species abundance models: geometric series, log normal, and broken stick. (b) Empirical rank/abundance plots (after Whittaker 1970). The three assemblages are nesting birds in a deciduous forest, West Virginia, vascular plants in a deciduous cove forest in the Great Smoky Mountains, Tennessee, and vascular plant species from subalpine fir forest, also in the Great Smoky Mountains. Comparison with (a) suggests that the best descriptors of these three assemblages are the broken stick, log normal, and geometric series, respectively – but see text for further discussion of this point. (Redrawn with kind permission of Kluwer Academic Publishers from fig. 2.4, Magurran 1988.)

illustrating changes through succession or following an environmental impact. Indeed, it is often recommended (see, for example, Krebs 1999) that the first thing an investigator should do with species abundance data is to plot them as a rank/abundance graph.

The shape of the rank/abundance plot is often used to infer which species abundance model best describes the data. Steep plots signify assemblages with high dominance, such as might be found in a geometric or log series distribution, while shallower slopes imply the higher evenness consistent with a log normal or even a broken stick model (Figure 2.5; see also below for further discussion of species abundance models). However, as Wilson (1991) notes, the curves of the different models have rarely been formally fitted to empirical data. Even Whittaker's (1970) well-known and widely reproduced log normal curve may have been fitted by eye (Wilson 1991). Wilson (1991) provides methods for fitting this and other models to rank/abundance (dominance/diversity) curves. These are discussed in the section (p. 43) on goodness of fit tests below.

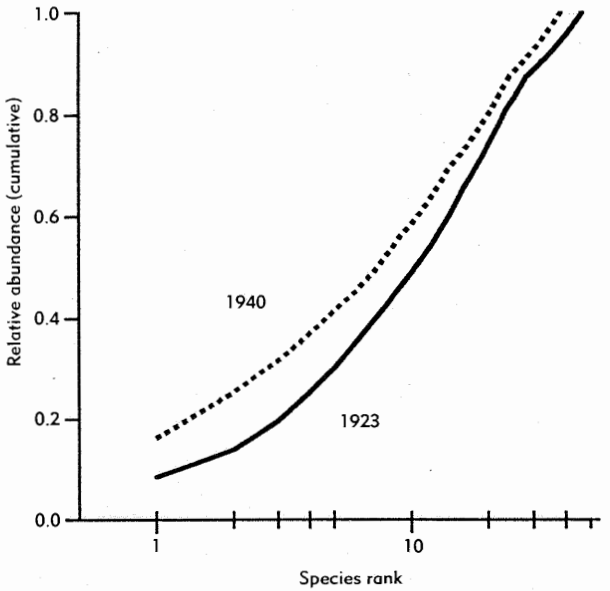

Figure 2.6 *k*-dominance plots for breeding birds at "Neotoma" (table II, Preston 1960). Censuses from 1923 and 1940 are compared. The latter plot is the more elevated, indicating that this assemblage is less diverse.

There are further ways of presenting species abundance data in a ranked format. For instance, the ***k*-dominance plot** (Lambshead *et al.* 1983; Platt *et al.* 1984) shows percentage cumulative abundance (*y* axis) in relation to species rank or log species rank (*x* axis) (Figure 2.6). Under this plotting method more elevated curves represent the less diverse assemblages. **Abundance/biomass comparison** or **ABC** curves (Figure 2.7), introduced by Warwick (1986), are a variant of the method. Here *k*-dominance plots are constructed separately using two measures of abundance: the number of individuals and biomass. The relationship between the resulting curves is then used to make inferences about the level of disturbance, pollution-induced or otherwise, affecting the assemblage (see Figure 5.8). The method was developed for benthic macrofauna and continues to be a useful technique in this context (see, for example, Kaiser *et al.* 2000), though it has been relatively little explored in others. ABC curves are revisited in Chapter 5 where their application in the measurement of ecological diversity will be considered. The *Q* statistic (Kempton & Taylor 1978; see also Chapter 4 and Figure 4.2) plots the cumulative number of species (*y* axis) against log abundance (*x* axis).

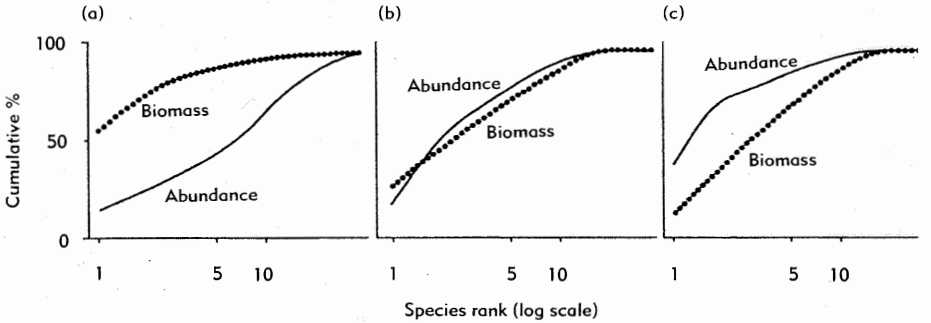

Figure 2.7 ABC curves showing expected *k*-dominance curves comparing biomass and number of individuals or abundance in (a) "unpolluted," (b) "moderately polluted," and (c) "grossly polluted" conditions. Species are ranked from most to least important (in terms of either number of individuals or biomass) along the (logged) *x* axis. They *y* axis displays the cumulative abundance (as a percentage) of these species. In undisturbed assemblages one or two species are dominant in terms of biomass. This has the effect of elevating the biomass curve relative to the abundance (individuals) curve. In contrast, highly disturbed assemblages are expected to have a few species with very large numbers of individuals, but because these species are small bodied they do not dominate the biomass. In such circumstances the abundance curve lies above the biomass curve. Intermediate conditions are characterized by curves that overlap and may cross several times. See Warwick (1986) for details, and Figure 5.8 which compares ABC curves for disturbed and undisturbed fish assemblages in Trinidad. (Redrawn with permission from Clarke & Warwick 2001a.)

Investigators of the broken stick model (for example, King 1964) often show relative abundance of species, in a linear scale, on the *y* axis and logged species sequences, in order from most abundant to least abundant, on the *x* axis. In this format a broken stick distribution is manifested as a straight line.

Other plotting methods are also popular. Advocates of the log series model, for example, have conventionally favored a frequency distribution in which the number of species (*y* axis) is displayed in relation to the number of individuals per species (Figure 2.8). A variant of this plot is typically employed when the log normal is chosen. Here the abundance classes on the *x* axis are presented on a log scale (Figure 2.9). This type of graph is sometimes dubbed a "Preston plot" (Hubbell 2001) in recognition of Preston's (1948) pioneering use of the log normal model. Each plotting method emphasizes a different characteristic of the species abundance data. In the conventional log series plot the eye is drawn to the many rare species and to the fact that the mode of the graph falls in the lowest abundance class (represented by a single individual). In contrast, the log transformation of the *x* axis often has the effect of

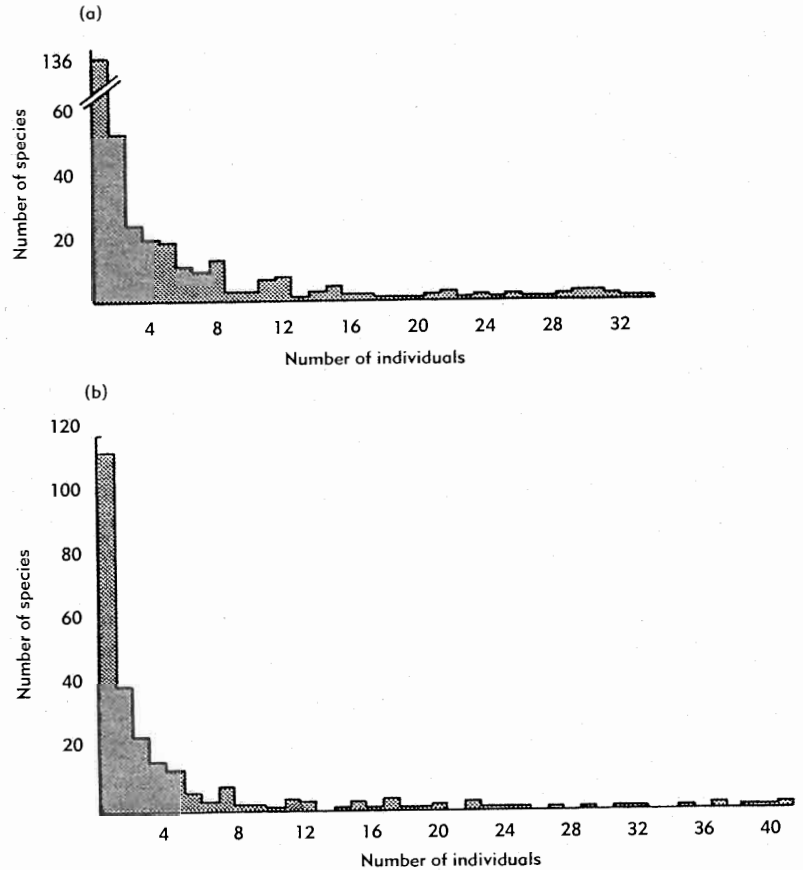

Figure 2.8 Frequency of species in relation to abundance. These graphs show the relationship between the number of species and the number of individuals in two assemblages: (a) freshwater algae in small ponds in northeastern Spain and (b) beetles found in the River Thames, UK. In both cases the mode falls in the smallest class (represented by a single individual). These graphs may be referred to as "Fisher" plots following R. A. Fisher's pioneering use of the log series model. (Redrawn with kind permission of Kluwer Academic Publishers from fig. 2.3, Magurran 1988; based on data from Williams 1964.)

shifting the mode to the right, thereby revealing a log normal pattern of species abundance.

In 1975 May argued that plotting methods needed to be standardized to facilitate the comparison of different data sets. In 1988 I concluded that there had been little progress towards that goal (Magurran 1988). None the less since that time the rank/abundance plot has gained in

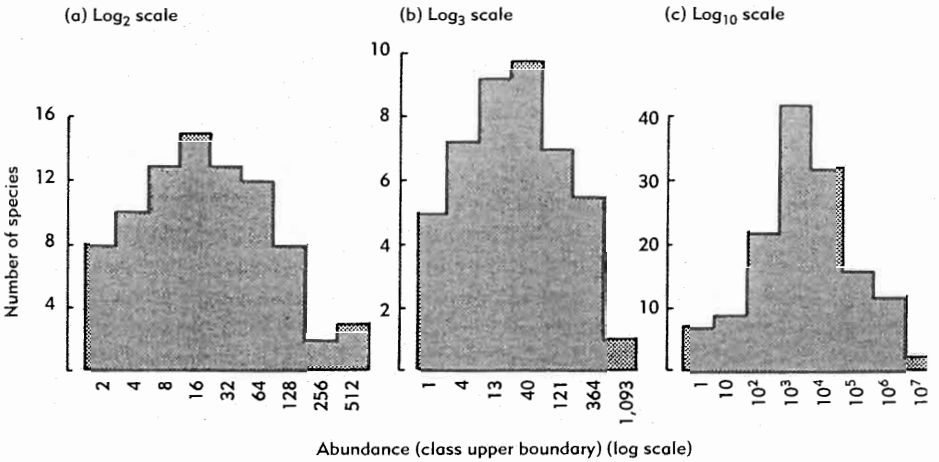

Figure 2.9 Frequency of species in relation to abundance. A "normal" bell-shaped curve of species frequencies may be achieved by logging species abundances. Three log bases (2, 3, and 10) have been used for this purpose. The choice of base is largely a matter of scale – it is clearly inappropriate to use $\log_{10}$ if the abundance of the most abundant species is $<10^2$ or to adopt $\log_2$ if it is $>10^6$. Less obviously, the selection of one base in preference to another can determine whether a mode is present. This is a crucial consideration since the presence of a mode is often used to infer "log normality" in a distribution. (The position of the class boundaries can also affect the likelihood of detecting a mode, see text for further details.) The figure illustrates three assemblages, each plotted using a different log base. (a) Log_2: diversity of ground vegetation in a deciduous woodland at Banagher, Northern Ireland. This usage follows Preston (1948). Species abundances are expressed in terms of doublings of the number of individuals. For example, successive classes could be ≤2 individuals, 3–4 individuals, 5–8 individuals, 9–16 individuals, and so on. It is conventional to refer to these classes as octaves. (b) Log_3: snakes in Panama. In this example the upper bounds of the classes are 1, 4, 13, 40, 121, 364, and 1,093 individuals. (c) Log_{10}: British birds. Classes in $\log_{10}$ represent increases in order of magnitude: 1, 10, 100, 1,000, and so on. In all cases the *y* axis shows the number of species per class. These graphs may be referred to as "Preston" plots. (Data in (b) and (c) from Williams 1964; redrawn with kind permission of Kluwer Academic Publishers from fig. 2.7, Magurran 1988.)

popularity (Krebs 1999). Perhaps standardization of methods is at last on the horizon.

Species abundance models

It is not simply plotting methods that have proliferated. A diverse range of models has also been developed to describe species abundance data. In essence there are two types. On one hand are the so-called **statistical** models, such as the log series (Fisher *et al.* 1943), that were initially devised as an empirical fit to observed data. The advantage of this type of

model is that it enables the investigator to objectively compare different assemblages. In some cases a parameter of the distribution, such as α in the case of the log series, can be used as an index of diversity. Alternatively, the goal may be to explain, rather than merely describe, the relative abundances of species in an assemblage. To do this it is necessary to predict how available niche space might be divided amongst the constituent species and then ask whether the observed species abundances match this expectation. Of course, there are many different ways in which resources might be subdivided amongst species and these **biological** or **theoretical** models represent different scenarios of niche apportionment. For example, Tokeshi's (1990, 1993) dominance pre-emption model envisages a situation where the niche space of the least abundant species in an assemblage is invariably invaded by a colonizing species. This contrasts with his dominance decay model in which the niche of the most dominant (that is the most abundant) species is targeted. The dominance pre-emption process generates a very uneven community in which the status of the most abundant species is preserved while the least abundant species lose resources and become progressively rarer over time. In contrast, Tokeshi's dominance decay model produces a community more even than the well-known broken stick model. These models are discussed in more detail below (see p. 50).

Although it is convenient to classify species abundance models as statistical or biological, in reality the distinction can be blurred (Table 2.1). Several of the statistical models, notably the log series and log normal (see below and p. 32), have acquired biological explanations since their original formulation. It is also important to remember that the fact that a natural community displays a species abundance relationship in line with the one predicted by a specific model does not in itself vindicate the assumptions on which the model is based. The conclusion that must be drawn in such cases is simply that the model cannot be rejected and that additional investigation, possibly including experimental manipulation, will be necessary for a fuller understanding of niche apportionment. Sampling may mask the true form of the species abundance distribution (Chapter 5). A further complication is that more than one biological or statistical model may describe the assemblage in question. This point is considered in detail on p. 43.

Statistical models

Log series

Fisher's logarithmic series model (Fisher *et al.* 1943) represented one of the first attempts to describe mathematically the relationship between the number of species and the number of individuals in those species.

Table 2.1 The classification of species abundance models (after Tokeshi 1993, 1999).

Type of model	Model	Reference
Statistical	Log series	Fisher *et al.* 1934
	Log normal	Preston 1948
	Negative binomial	Anscombe 1950
		Bliss & Fisher 1953
	Zipf–Mandelbrot	Zipf 1949
		Mandelbrot 1977
		Mandelbrot 1982
Biological		
Niche based	Geometric series	Motomura 1932
	Particulate niche	MacArthur 1957
	Overlapping niche	MacArthur 1957
	Broken stick	MacArthur 1957
	MacArthur fraction	Tokeshi 1990
	Dominance pre-emption	Tokeshi 1990
	Random fraction	Tokeshi 1990
	Sugihara's sequential breakage	Sugihara 1980
	Dominance decay	Tokeshi 1990
	Random assortment	Tokeshi 1990
	Composite	Tokeshi 1990
	Power fraction	Tokeshi 1996
Non-niche based	Dynamic model	Hughes 1984, 1986
Other	Neutral model	Caswell 1976
	Neutral model	Hubbell 2001

Although originally used as a convenient fit to empirical data, its wide application, especially in entomological research, has led to a thorough examination of its properties (Taylor 1978), as well as speculation about its biological meaning (see below). The log series model is straightforward to fit (Worked example 1). One of its parameters, α, has proved an informative and robust diversity measure (Chapter 4).

The log series takes the form:

$$\alpha x, \frac{\alpha x^2}{2}, \frac{\alpha x^3}{3}, \ldots \frac{\alpha x}{n}$$

with αx being the number of species predicted to have one individual, $\alpha x^2/2$ those with two, and so on (Fisher *et al.* 1943; Poole 1974). Since $0 < x < 1$, and both α and x are constants (for the purposes of fitting the model to a specified data set), the expected number of species will be greatest in the smallest abundance class (of one individual) and decline thereafter. It should also be noted that the log series distribution, in contrast to many other models, expects that species abundance data will come in the form of numbers of individuals. The log series is therefore inappropriate if

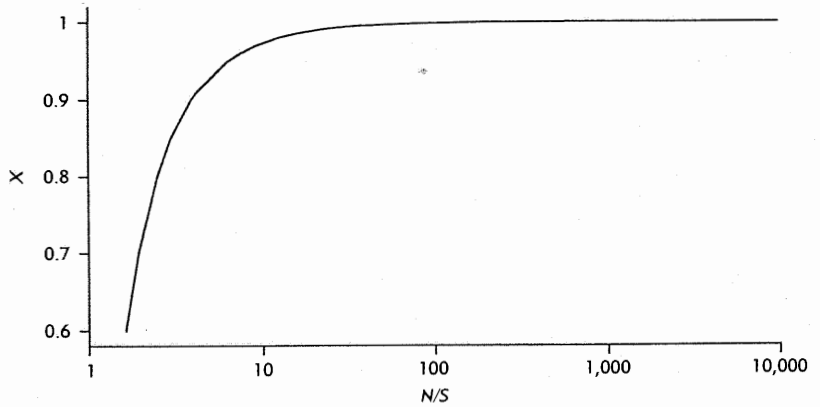

Figure 2.10 Values of x in relation to N/S. See text for details.

biomass or some other noninteger measures of abundance is used. Hayek and Buzas (1997) explain how to fit the model using occurrence (frequency) data.

x is estimated from the iterative solution of:

$$S/N = [(1-x)/x] \cdot [-\ln(1-x)]$$

where N is the total number of individuals.

In practice x is almost always >0.9 and never >1.0. If the ratio N/S >20 then x >0.99 (Poole 1974). Krebs (1999, p. 426) lists values of x for various values of N/S. This relationship is illustrated in Figure 2.10.

Two parameters, α, the log series index, and N, summarize the distribution completely, and are related by:

$$S = \alpha \ln(1 + N/\alpha)$$

where α is an index of diversity. Indeed, since x often approximates to 1, α represents the number of extremely rare species, where only a single individual is expected.

α has been widely used, and remains popular (Taylor 1978) despite the vagaries of index fashion. It is also a robust measure, as well as one that can be used even when the data do not conform to a log series distribution (see Chapter 4 for a discussion of α as a diversity measure).

The index may be obtained from the equation:

$$\alpha = \frac{N(1-x)}{x}$$

with confidence limits set by:

$$\mathrm{var}(\alpha) = \frac{0.693147\alpha}{[\ln(x/(1-x)) - 1)]^2}$$

as proposed by Anscombe (1950). Note that 0.693147 = ln 2. Both Hayek and Buzas (1997) and Krebs (1999) provide more details. Hayek and Buzas (1997) advise that this formula should not be used when $N/S \leq 1.44$ or when $x \leq 0.50$. However, as such values are atypical, this restriction is unlikely to be burdensome.

As values of α are normally distributed, attaching confidence limits to an estimate of α is simple (Hayek & Buzas 1997). The first step is to obtain the standard error of α by taking the square root of the variance. (Hayek and Buzas (1997) remind us that because we are dealing with the sampling variance of a population value, taking the square root of the variance produces the standard error rather than the standard deviation.) This standard error can then be multiplied by 1.96 to yield 95% confidence limits.

Alternatively, α can be deduced from values of S and N using the nomograph provided by Southwood and Henderson (2000), following Williams (1964).

To fit the log series model itself one simply calculates the number of species expected in each abundance class and, using a goodness of fit test (see p. 43), compares this with the number of species actually observed (see Worked example 1).

It should also be noted that the log series can arise as a sampling distribution. This will occur if sampling has been insufficient to fully unveil an underlying log normal distribution (see Figure 2.14 for more explanation).

Although the log series was initially proposed as a statistical model, that is one making no assumptions about the manner in which species in an assemblage share resources, its wide application prompted biologists to consider the ecological processes that might underpin it. These are most easily reviewed in relation to the geometric series (discussed below in the context of niche apportionment models), to which the log series is closely related (May 1975). A geometric series distribution of species abundances is predicted to occur when species arrive at an unsaturated habitat at regular intervals of time, and occupy fractions of remaining niche space. A log series pattern, by contrast, will result if the intervals between the arrival of these species are random rather than regular (Boswell & Patil 1971; May 1975). The log series produces a slightly more even distribution of species abundances than the geometric series, though one less even than the log normal distribution (see below). The small number of abundant species and the large proportion of "rare"

species predicted by the log series imply that, as is the case with the geometric series, it will be most applicable in situations where one or a few factors dominate the ecology of an assemblage. For instance, I found that the species abundances of ground flora in an Irish conifer woodland, where light is limited, followed a log series distribution (Magurran 1988) (Figure 2.11). In can be hard to distinguish between these models in terms of their fit to empirical data. Thomas and Shattock (1986), for example, showed that both the geometric series and the log series models adequately described the species abundance patterns of filamentous fungi on the grass *Lolium perenne*.

Log normal

Distribution

The log normal distribution was first applied to abundance data by Preston in 1948 in his classic paper on the commonness and rarity of species. Preston plotted species abundances using $\log_2$ and termed the resulting classes "octaves." These octaves represent doublings in species abundance (see, for example, Figure 2.9). It is not, however, necessary to use $\log_2$; any log base is valid and $\log_3$ and $\log_{10}$ are two common alternatives (Figure 2.9). May (1975) provides a thorough and lucid discussion of the model.

The distribution is traditionally written in the form:

$$S(R) = S_0 \exp(-a^2 R^2)$$

where $S(R)$ = the number of species in the Rth octave (i.e., class) to the right, and to the left, of the symmetric curve; S_0 = the number of species in the modal octave; and $a = (2\sigma^2)^{-1/2}$ = the inverse width of the distribution.

Empirical studies show that a is usually ≈0.2 (Whittaker 1972; May 1975). A further parameter of the log normal, γ, emerges when a curve of the number of individuals in each octave, the so-called individuals curve, is superimposed on the species curve of the log normal (Figure 2.12). It is defined as:

$$\gamma = R_N / R_{\max} = \ln 2 / \left[2a (\ln S_0)^{1/2}\right]$$

where R_N = the modal octave of the individuals curve; and $R_{\max}$ = the octave in the species curve containing the most abundant species (May 1975).

In many cases the crest (or mode) of the individuals curve (R_N) coincides with the upper tail of the species curve ($R_{\max}$) to give $\gamma \approx 1$. (This

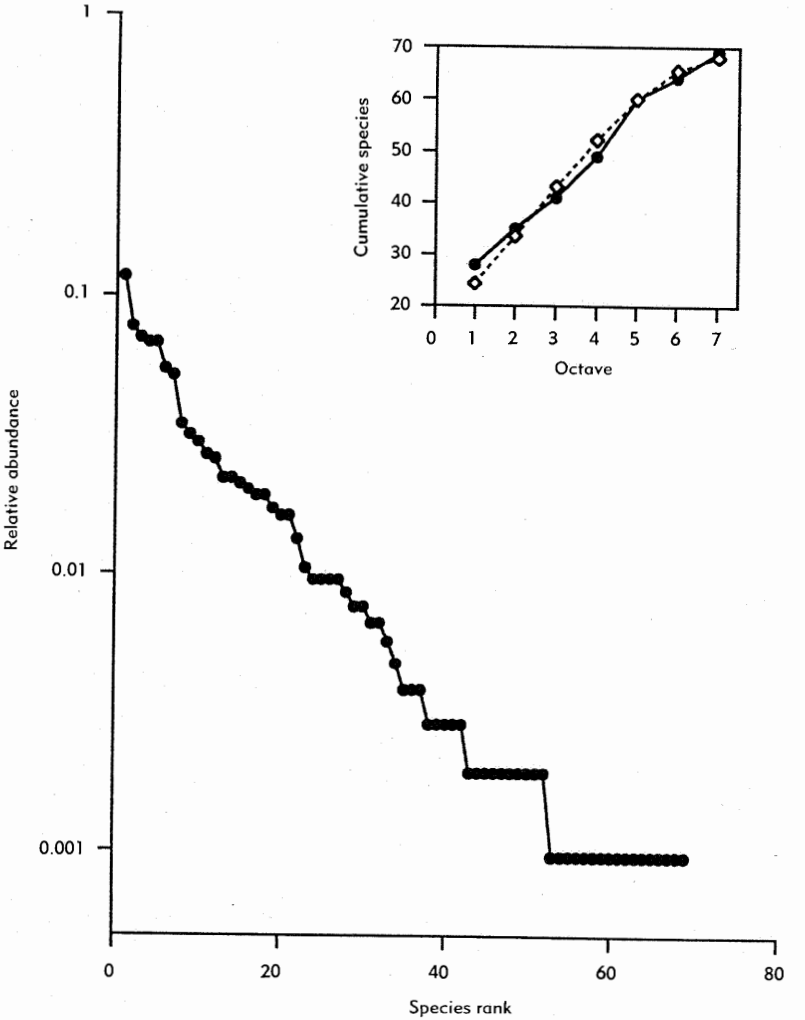

Figure 2.11 Rank/abundance plot of ground vegetation in an Irish conifer plantation. The slope of the graph is indicative of a log series distribution. The inset shows the cumulative observed (solid line) and expected (dotted line) number of species in relation to abundance class (in octaves) for the same data set. The congruence between the observed and expected distributions confirms that the data do indeed follow a log series ($D = 0.06$, $P > 0.05$, Kolmogorov–Smirnow test; see Worked example 1).

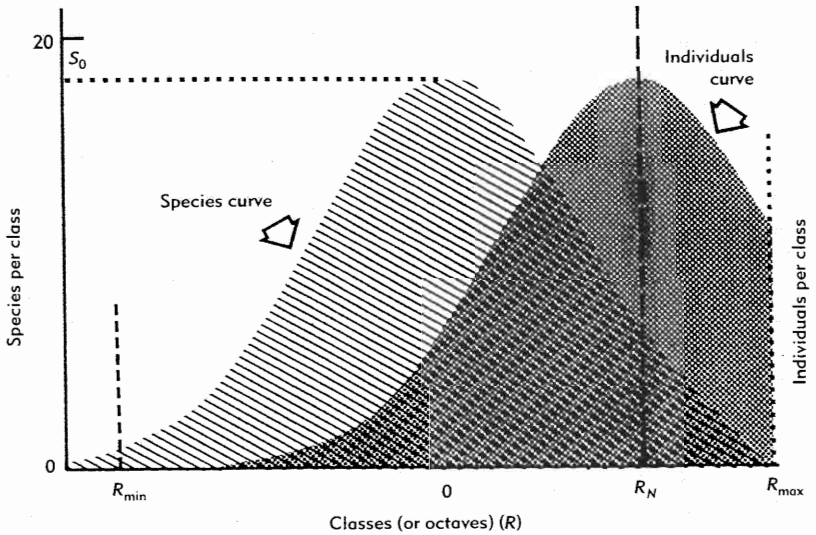

Figure 2.12 Features of the log normal distribution. The striped curve (species curve) shows the distribution of species amongst classes. If these classes are in $\log_2$ – that is doublings in numbers of individuals – they are referred to as octaves (see Figure 2.9). Since the distribution is symmetric, classes in the same position on either side of the mode are expected to have equal numbers of species. For this reason it is conventional to term the modal class 0 and to refer to classes to the right of the mode as 1, 2, 3, etc. and those on its left hand side as –1, –2, –3, etc. R_{min} marks the position of the least abundant species while R_{max} shows the expected position of the most abundant species. ($R_{max} = -R_{min}$.) The number of species in each class is $S(R)$. In this example the number of species in the modal class (S_0) would be 18. The species curve can be superimposed by the individuals curve (hatched) representing the number of individuals present in each class. The class with the most individuals (in other words the one in which the mode of the individuals curve occurs) is termed R_N. A log normal distribution is described as canonical when R_N and R_{max} coincide to give the value $\gamma = 1$ (where $\gamma = R_N/R_{max}$). (Redrawn with kind permission of Kluwer Academic Publishers from fig. 2.12, Magurran 1988, after May 1975.)

simply means that there are more individuals in class R_{max} than in any other class; it is an empirical rule that holds true for many different data sets.) In such log normals, described by Preston (1962) as "canonical" (Preston's canonical hypothesis), the standard deviation is constrained between narrow limits (resulting in $a \approx 0.2$). In other words, the standard deviation (s.d.) of species abundances in reasonably large assemblages ($S > 100$), when these abundances are expressed in a $\log_2$ scale, is around 4. Nee *et al.* (1992, 1993) show why this makes biological sense. They note that, given a log normal distribution, 99% of species would be expected to occur within ±3 s.d. of the mean. Thus, should the standard deviation be 4, the range of abundances will be 2^{24}. This can be illustrated

as follows. The 6 s.d. needed to encompass 99% of species are multiplied by the value of the standard deviation (4) to give 24, and because a $\log_2$ scale is being used to measure abundance, the range of these abundances is 2^{24}. Since the abundance of the least abundant species is 1, the most abundant will have 16,777,216 individuals. This number is plausible for many taxa. On the other hand, larger standard deviations generate upper limits of abundance that are unlikely to be met. If, for example, the standard deviation is 7.5, the most abundant species would have $3.5 * 10^{13}$ individuals, an improbable tally for most vertebrates at least. If high levels of abundance can genuinely be achieved, as seems to be the case for taxa such as diatoms (Hutchinson 1967; Nee *et al.* 1992), and the standard deviation remains around 4 (Sugihara 1980), the implication is that the abundance of the least abundant species is also considerable. It is relatively easy to explain why the standard deviation will rarely be much greater than 4, but what prevents it from being considerably less? Why are the most abundant species not just twice, or even 10 times as abundant as the rarer ones? Nee *et al.*'s (1992) answer is that basic differences in biology between species, including niche requirements and trophic level, inevitably generate substantial differences in abundance.

Statistical and biological explanations for the log normal

The majority of large assemblages studied by ecologists appear to follow a log normal pattern of species abundance (May 1975; Sugihara 1980; Gaston & Blackburn 2000; Longino *et al.* 2002) and many of these log normal distributions can be described as canonical. Such pervasive patterns invariably prompt a search for ecological explanations. May (1975), however, notes that many other large data sets, such as the distribution of human populations in the world, as well as of wealth within countries such as the USA, are log normal in character. He attributes the near ubiquity of the log normal, and the prevalence of its canonical form, to the mathematical properties of large data sets. May (1975) points out that the log normal is a consequence of the central limit theorem, which states that when a large number of factors act to determine the amount of a variable, random variation in those factors will result in the variable being normally distributed. This effect becomes more pronounced as the number of determining factors increases. In the case of log normal distributions of species abundance data, the variable is the number of individuals per species (standardized by a log transformation) and the determining factors are all the processes that govern community ecology (but see also Pielou 1975; Gaston & Blackburn 2000). Speciose assemblages (with $S > 200$) are particularly likely to be canonical (Ugland & Gray 1982). Ugland and Gray (1982) have also argued that ecological processes need not be invoked to explain the canonical log normal.

Others have none the less advocated a stronger biological underpinning. Sugihara (1980) argued that many natural assemblages, including those of birds, moths, gastropods, plants, and diatoms, fit the canonical hypothesis too well for it to be a statistical artifact. Following Pielou (1975), Sugihara (1980) developed a model in which niche space is sequentially split into S pieces. A split occurs each time a new species invades the assemblage and competes for existing resources. During each invasion an existing niche is targeted at random. This means that all niches, irrespective of their size, are equally likely to be selected for division (in other niche-based models such as MacArthur's broken stick and Tokeshi's power fraction the probability that a niche will be selected for splitting is some function of its size; see p. 55). If a niche is broken at random the larger of the two fragments will represent between 50% and 100% of its original size. On average, then (after many such divisions), the larger of the new niches will be 75% of the old one. Sugihara represented this by assuming a 75% : 25% split at each division. The outcome resembles a canonical log normal distribution.

This approach treats the log normal distribution as one of niche apportionment—that is a biological model—rather than the statistical model it was initially conceived as. Indeed Tokeshi (1999) notes that Sugihara's model can be viewed as a special case of the random fraction model (described below), albeit with some important distinctions (see Tokeshi (1996, 1999) for details, and a critique of some of Sugihara's assumptions). Drozd and Novotny's (2000) PowerNiche program can be used to calculate expected species abundances.

Unveiling the distribution

In addition to the conceptual difficulty of deciding whether, and to what extent, the log normal might encapsulate biological processes, investigators face practical problems in fitting it to empirical data. Like its normal sibling, the log normal distribution is a symmetric, bell-shaped curve. If, however, the data to which the curve is to be fitted derive from a sample, the left-hand portion of the curve, representing the rare and harder to sample species, may be obscured. Preston (1948) termed the truncation point of the curve the **veil line** and argued that the smaller the sample the further this veil line will be from the origin of the curve (Figure 2.13). In many data sets only the portion of the curve to the right of the mode is visible. It is only in large data collections, such as those covering wide biogeographic areas or derived from long periods of intensive sampling, that the full curve is likely to be revealed. Longino *et al.*'s (2002) investigation of ant species at La Selva in Costa Rica provides a good example. Some 1,904 samples were collected using various methods. When these are plotted to represent successive doublings of

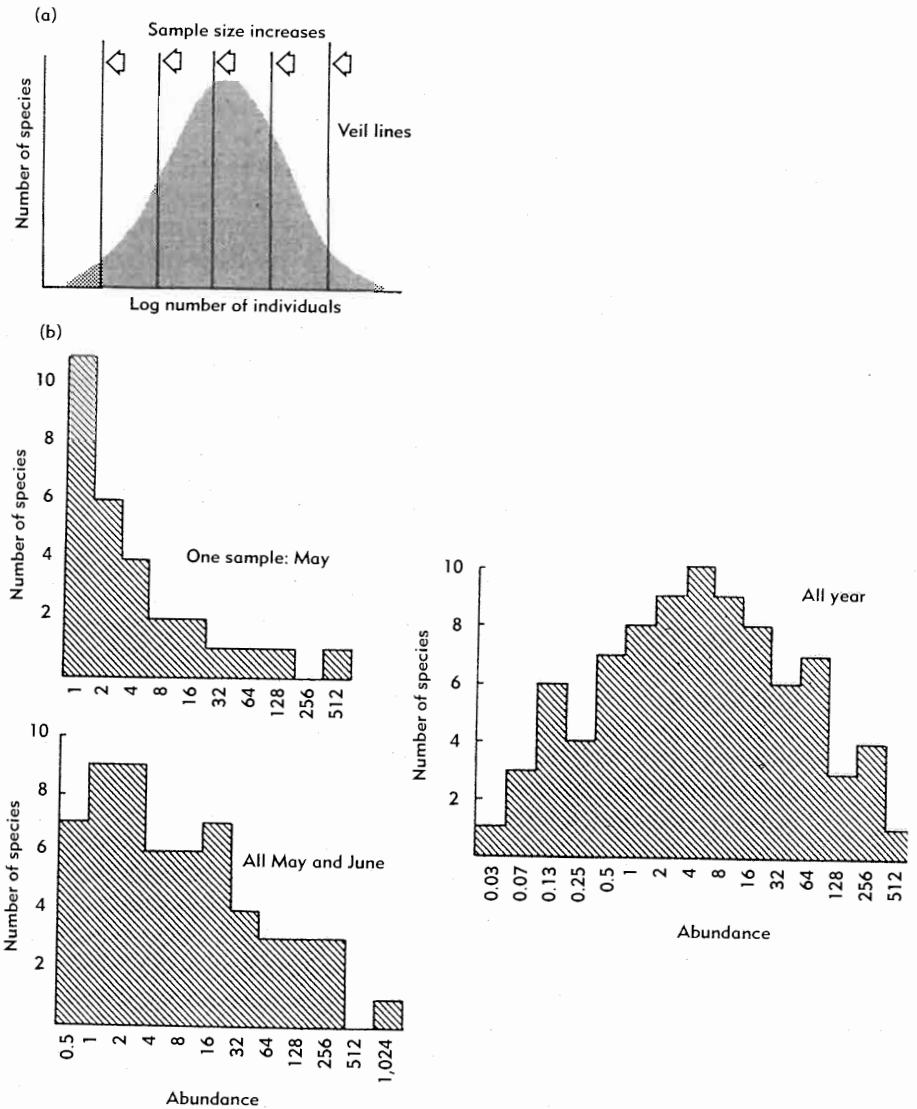

Figure 2.13 The veil line. (a) In small samples, only the portion of the distribution to the right of the mode may be apparent. However, as sample size increases the veil line is predicted to move to the left revealing first the mode and eventually the entire distribution. This effect is evident in (b). (b) Fish diversity in the Arabian Gulf. Samples of fish were collected in an area of the Gulf adjacent to Bahrain. Abundance – the mean number of individuals caught in 45 min trawling – is shown in $\log_2$ classes (octaves). In single samples, for instance one caught in May, only the right hand portion of the log normal distribution is evident. Once the samples taken throughout May and June are included the mode becomes apparent. The full log normal distribution is revealed when data collected for the entire year are used. A similar effect can be seen in Figure 2.14. (Redrawn with kind permission of Kluwer Academic Publishers from fig. 2.10. Magurran

sampling effort a log normal distribution is progressively unveiled (their figure 4). Immense samples are no guarantee of an unveiled log normal, however. Preston (1948) described two long-term data collections in his original paper. The first of these, a sample of moths collected at Saskatoon in Canada over 22 years, numbered 277 species and more than 87,000 individuals. Preston used the position of the veil line to predict that it was only 72% complete. His second example, another collection of moths, again spanning 22 years and consisting of 291 species and over 300,000 individuals, also had a veil line and was estimated to be 88% complete. It is sometimes argued that such broadly based collections of data contain such a multiplicity of assemblages as to render them ecologically uninterpretable. Wilson (1991) believes that because plant biomass is so plastic, there is no lower limit to the abundance of a species in a community and accordingly that the veil line is inapplicable to plants.

A fully unveiled distribution can be fitted, without complications, using standard procedures. Partly veiled distributions are more problematic. It is sensible not to attempt to fit a log normal to a truncated distribution unless the mode of this distribution is apparent. This seems obvious advice until one realizes that a mode can be revealed or obscured depending on which log base is used to construct the abundance classes (Hughes 1986), or even by the precise manner in which boundaries between the abundance classes are assigned (as noted by Colwell & Coddington 1994). Providing the investigator is convinced that it is prudent to proceed, a truncated log normal can be fitted using the approach outlined by Pielou (1975), following Cohen (1959, 1961). The species abundances are logged ($x = \log_{10} n_i$) and a normal curve fitted, disregarding the area to the left of the truncation point. The truncation point is assumed to fall at –0.30103 or $\log_{10} 0.5$, this being the lower boundary of the class containing species for which only one individual was observed. Table 1 in Cohen (1961) (reproduced in Magurran (1988) and Krebs (1999)) provides θ, the function needed to estimate the mean and variance of the truncated distribution. Once these values are calculated, the expected frequencies of species in each abundance class can be obtained and compared with observed frequencies using a goodness of fit test (see p. 43). Krebs (1999) has written a PC Windows-based computer program[3] that fits a truncated log normal according to Pielou's (1975) method. However, it can also be fitted using a spreadsheet (see Worked example 2 for an example).

The area under the curve provides an estimate of S^*, the total number of species in the assemblage. (These estimates of S^* should be treated with extreme caution. More effective methods of estimating species

3 This program, and others relating to the methods described in Krebs (1999), can be obtained from www.exetersoftware.com.

richness are described in the next chapter.) Further discussion of the truncated log normal is provided by Slocomb *et al.* (1977).

Strictly speaking, the continuous log normal described here (whether truncated or not) should only be applied to continuous abundance data, such as biomass or cover measures, rather than to discrete data, including numbers of individuals. In practice, however, most people use the continuous log normal when abundances have been measured as numbers of individuals since, for large sample sizes especially, these data are effectively continuous.

An alternative method of fitting a log normal distribution to sample data has been discussed by Bulmer (1974) and Kempton and Taylor (1974) and is referred to as either the Poisson log normal or the discrete log normal. It is assumed that the continuous log normal is represented by a series of discrete abundance classes which behave as compound Poisson variates. The Poisson parameter λ is distributed log normally. Although the Poisson log normal presents greater computational difficulties than the continuous log normal, the greater availability of computer packages capable of fitting it mean that, for many, this is not a serious impediment. The Poisson log normal also provides an estimate of S^*, to which, in contrast with the estimate generated by Pielou's method, confidence limits can be attached. Given the omnipresence of the log normal distribution this estimate of S^* appears to offer a promising method of deducing overall species richness in incompletely sampled assemblages. Unfortunately, as the next chapter shows, the confidence limits are often so large that such estimates are meaningless.

One might also expect that σ, the standard deviation, of the log normal distribution would be a useful measure of diversity. Although σ can be treated as a measure of evenness it is an ineffective discriminator of samples, and cannot be estimated accurately when sample size is small (Kempton & Taylor 1974). These criticisms do not, however, apply to the ratio $S^* : \sigma$, referred to as λ. There is a marked correlation between the values of λ and α calculated for the same data and both are good at discriminating amongst samples and assemblages (Kempton & Taylor 1974; Taylor 1978). Further details are provided in Chapter 4.

In addition to statistical fits there are, of course, graphic methods for deciding whether data are log normally distributed. The simplest of these, already noted, is to examine a graph in which the species frequency is plotted against log abundance classes. (See, for example, Figures 2.9 and 2.13.) Alternatively, a "probability plot" (Gray 1979, 1981; Gray & Mirza 1979)—in which abundance (in $\log_2$ classes) is shown on the x axis and cumulative frequency of species on the y axis—can be used to detect the presence of a log normal distribution, as well as departures from it. Log normal distributions appear as straight lines on such a graph and the method has been used to assess the effects of pollution on marine

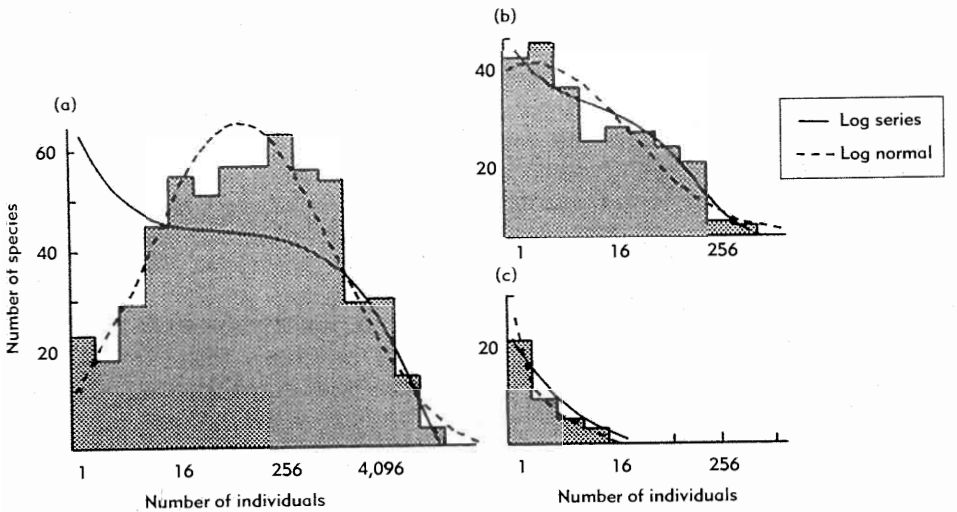

Figure 2.14 The relationship between log series and log normal distributions. These three graphs show: (a) the abundance of moths summed across 225 sites through Britain, (b) a typical annual sample from a single rural site, and (c) a sample from an impoverished urban site. The dashed lines represent log normal distributions fitted to the data. Log series distributions are indicated by continuous lines. These graphs demonstrate how small samples (in which the full log normal distribution is apparently veiled) are described equally well by both the log series and (truncated) log normal. When the complete log normal distribution is revealed the log series ceases to be a good fit. (Redrawn with permission from Taylor 1978.)

benthic communities (Gray 1979). Since large natural assemblages are typically log normal in character any departures from a log normal distribution ought to be indicative of disturbance. However, Tokeshi (1993) has criticized the method as being insensitive to changes in species richness, and rather poor at discriminating species abundance distributions. Indeed, he notes that a geometric series distribution, the pattern typically associated with a polluted or perturbed assemblage, also appears as a straight line of this type of graph.

Overlapping distributions

Many data sets are described equally well by both the log series and (truncated) log normal making it impossible to decide which model is more appropriate. Figure 2.14 illustrates why the log series is sometimes regarded as a sampling distribution, which could, with greater effort, be extended to reveal the underlying (unveiled) log normal. Since the log normal describes more data sets than the log series, and may encapsulate

the many processes at work in ecology, it is arguably the most suitable vehicle for comparing assemblages (May 1975). On the other hand, Kempton and Taylor (1978) and Taylor (1978) favor the log series distribution because it accentuates the "median range" of commonness. This property helps insure that α is a robust diversity index (see also Chapter 4).

The contention that the log normal is the default distribution for large and unperturbed communities has not gone unchallenged. Lambshead and Platt (1985) argue that many classic data sets are not true samples, but rather collections or amalgamations of nonreplicate samples. Furthermore, they assert that the shape of the log normal distribution is independent of sample size, and conclude that "the log normal . . . is never found in genuine ecological samples" and advocate the adoption of the log series model instead. Tokeshi (1999) also questions the generality of the log normal. Following Nee *et al.* (1991), he notes that many species-rich assemblages are characterized by a high proportion of rare species. These produce plots that are skewed to the left (Hubbell & Foster 1986; Gaston & Blackburn 2000; see also Figure 2.9). Tokeshi postulates that such truncated distributions are in fact true representations of the underlying pattern of species abundance in diverse assemblages and that a symmetric log normal pattern will never emerge, irrespective of the intensity with which the assemblage is sampled. Indeed, Tokeshi (1999) suggests that in future it may be necessary to turn to niche apportionment models in order to explain abundance patterns in these and other communities. Gaston and Blackburn (2000) also assert that large-scale assemblages, including those that have been thoroughly surveyed (such as British birds), are often log left-skewed. They note that Tokeshi's (1996) power fraction model and Hubbell's (2001) neutral theory (both discussed in more detail later in this chapter), along with Harte *et al.*'s (Harte & Kinzig 1997; Harte *et al.* 1999a) self-similarity model, produce distributions with more rare species than the log normal would predict. Sugihara's (1980) model also generates a log left-skewed distribution (Nee *et al.* 1991).

Peter Henderson and I (Magurran & Henderson 2003) offer a different solution to this problem. We note that communities can be dissected into two components: permanent members versus occasional species. This partition requires either a long-term data series or good biological knowledge of the species themselves. The distribution of permanent species typically resembles a log normal whereas occasional species tend to follow a log series distribution of species abundance (Figure 2.15). The prominence of this log series distribution reflects the importance of the migratory or infrequent component of the assemblage. Interestingly, the assumptions that Fisher *et al.* (1943) made when they first applied the log series distribution to species abundance data anticipate this out-

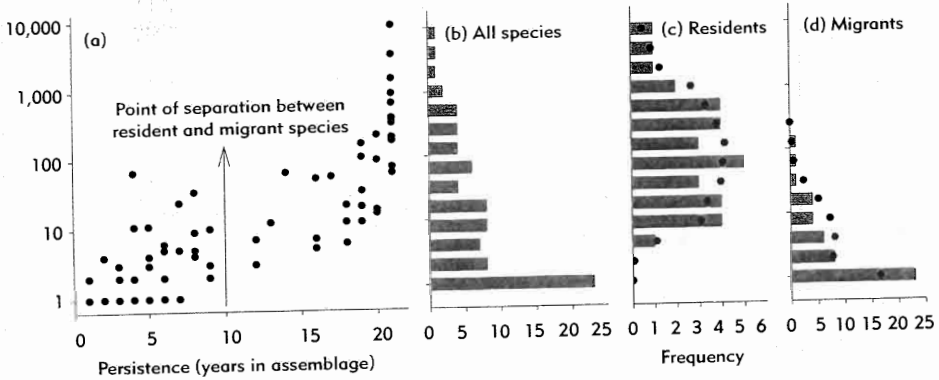

Figure 2.15 The pattern of abundance and persistence in a estuarine fish assemblage (Bristol Channel, UK). The data are for a 21-year time series of monthly samples. (a) The number of years in which each fish was observed, plotted against the maximum abundance in any one year. A discontinuity (indicated by the vertical arrow) allows the resident and migrant species to be defined as those present in >10 years and <10 years. (b) The abundance distribution for all species. (c) The abundance distribution of the resident species. The frequency of each abundance class predicted by the log normal model is shown as a dot ($\chi^2_{[6]}=0.88$, $P=0.99$). (d) The abundance of the occasional species; the frequency of each abundance class predicted by a log series model is shown by a dot ($\chi^2_{[6]}=4.24$, $P=0.39$). (Redrawn with permission from Magurran & Henderson 2003.)

come. When these distributions are superimposed, a log left-skewed distribution is the result. Like Hubbell (2001)—but through a different line of reasoning—we conclude that level of migration is the key to explaining the characteristic left skew of log-transformed species abundance distributions.

Other statistical models

The **negative binomial** model has many applications in ecology (Southwood & Henderson 2000), including species richness estimation (Coddington *et al.* 1991) but, as Pielou (1975) remarked, it is only rarely fitted to species abundance data (one exception being Brian (1953)). Given the plethora of competing models this alone seems sufficient reason not to revive it. Yet, the negative binomial is of potential interest since it comes from the same stable of models as the log series. (The log series is in fact a limiting form of the negative binomial.) Pielou (1975) provides more details, including a method of fitting the negative bionomial to observed data.

The **Zipf–Mandelbrot** model (Zipf 1949, 1965; Mandelbrot 1977, 1982; Gray 1987), on the other hand, has attracted more interest. Like the Shannon diversity index (Chapter 4), this approach has its roots in linguistics and information theory. It has been interpreted as reflecting a successional process in which later colonists have more specific requirements and hence are rarer than the first species to arrive (Frontier 1985). The model postulates a rigid sequence of colonists, with the same species always present at the same point in the succession in similar habitats. This prediction is patently not followed in the real world and Tokeshi (1993) considers the model no more biological than the log normal or log series. None the less, the model has been successfully applied in a number of studies (Reichelt & Bradbury 1984; Frontier 1985; Gray 1987; Barange & Campos 1991), and continues to have application in both terrestrial (Watkins & Wilson 1994; Wilson *et al.* 1996; Mouillot & Lepetre 2000) and aquatic (Juhos & Voros 1998) systems. It has also been used to test the performance of various diversity estimators (Mouillot & Lepetre 1999).

Goodness of fit tests

The conventional method of fitting a deterministic model is to assign the observed data to abundance classes. Classes based on $\log_2$ are often used. These represent doublings of abundance—2, 4, 8, 16, 32, etc., individuals—are intuitively meaningful, and typically produce a manageable number of classes. If abundance data are in the form of numbers of individuals, adding 0.5 to the class boundaries means that species can be allocated to abundance classes without ambiguity. The number of species expected in each abundance class is calculated according to the model used. (The model takes the observed values of S (number of species) and N (total abundance) and then determines how these N individuals should be distributed amongst the S species.) A goodness of fit test, often χ^2 but sometimes G (Sokal & Rohlf 1995), is used to evaluate the relationship between the observed and expected frequencies of species in each abundance class. If $P<0.05$ the model can be rejected, that is it not does adequately describe the pattern of species abundances. If $P>0.05$, or ideally $P>>0.05$, then a fit can be assumed.

There are drawbacks associated with using goodness of fit tests in this way. Tests of empirical data typically involve a small number of abundance classes, perhaps 10 or fewer. This restricts the degrees of freedom (d.f.) available. These must then be reduced (by 1 in the case of the geometric series and log series and by 3 for the truncated log normal) to allow for the parameters required by the model. The number of classes, and thus the degrees of freedom, may need to be pruned further if the number of species expected in a given class is small (<1). Recall that the formula for χ^2 is [(observed – expected)^2/expected] and that this calculation is summed across the classes. If expected frequencies fall below 1, χ^2 will

return an unrealistically high value. To circumvent this problem the user can sum the expected values in adjacent classes (and their observed equivalents) and adjust the degrees of freedom as appropriate (see Magurran (1988) for some examples). The more the degrees of freedom are eroded, the harder it becomes to reject a model. This difficulty is compounded by the fact that the differences between the models can lie in the way they allocate species to two or three abundance classes.

One solution might be to use the whole χ^2 distribution when comparing fits of various models. For example, if goodness of fit tests gave values of $\chi^2 = 10.5$ (with 6 d.f.) for the truncated log normal, and $\chi^2 = 2.8$ (with 8 d.f.) for the log series, it would be possible to make the statement that the probability of the expected log normal being different from the observed data is <90%, while the probability of the log series being different is <10%. Both values are below the conventional level of 95% but the log series clearly provides a better description of the data. However, Wilson (1991) cautions that unless the models can be viewed as subsets of one another, it would be invalid to conclude that one was a significantly better fit. In principle it is possible to use a power test to determine whether the sample size is sufficient to allow a particular species abundance model to be rejected, but in practice this approach has been little used.

Tokeshi (1993) also notes that goodness of fit tests work most effectively with large assemblages ($S > 100$), but is concerned that such assemblages might not be ecologically coherent units. Instead of χ^2 he recommends the Kolmogorov–Smirnov goodness of fit (GOF) test (Siegel 1956; Sokal & Rohlf 1995). Like the χ^2 test it can be used to assess the congruence between observed data and a theoretical expectation, and, in contrast to the χ^2 test, it may be applied to very small samples. Indeed, Tokeshi (1993) advocates adopting the Kolmogorov–Smirnov GOF test (Sokal & Rohlf 1995) as the standard method of assessing the goodness of fit of deterministic models. (He also suggests the Kolmogorov–Smirnov two-sample test can be used to compare two data sets directly, independently of any attempt to formally describe their abundance patterns—see Worked example 3 and general recommendations below.)

Wilson (1991) provides methods for fitting rank/abundance data to the log normal, geometric series, broken stick, and Zipf–Mandlebrot models. These involve minimizing the deviance between the observed and fitted rank/abundance plots. Once again the issue of goodness of fit arises. Wilson (1991) reinforces the earlier observation (Frontier 1985; Lambshead & Platt 1985; Hughes 1986; Magurran 1988) that a single data set will often be equally well described by several models. Furthermore, he notes that if one model fits the data, and another does not, it is not possible to conclude that the fit of the two is significantly different. His solution is to use replicated observations, since these increase the probability that the assemblage has been adequately described. (The same advice comes from Tokeshi (1993).) Wilson then recommends that an objective test would be analysis of variance on the abundance model x replicate table of deviances, with the model x replicate interaction providing the error term. The deviances can be log transformed, if necessary, to achieve normality. A multiple comparison test, for example Duncan's new multiple range test (see Sokal and Rohlf (1995) for further examples), can then be used to infer which models are significantly different from one another.

Biological (or theoretical) models

The search for biologically based models has a venerable tradition. Although Motomura's (1932) geometric series was initially proposed as a statistical model, later investigators (see Tokeshi 1993, 1999 for a discussion) realized that it is a metaphor for the way colonists in an ecological community might divide the available niche space between them. R. H. MacArthur (1957) was the first to explicitly challenge the use of statistically based models and devised three niche apportionment models. Two of these, the particulate niche and the overlapping niche, were considered unsatisfactory by MacArthur himself, but his third model, the broken stick, has played a significant role in shaping the way ecologists think about the diversity of ecological communities. The broken stick model continues to have application today, often as a null hypothesis against which other patterns of niche division can be tested. That was essentially how things stood until Tokeski (1990, 1993, 1999) took another look at niche apportionment models and devised a number of new ones, including some that appear to offer considerable potential.

Biological models are based on the assumption that an ecological community has a property called niche space that is divided amongst the species that live there. Although niche space is most easily visualized in one or two dimensions, niches, as Hutchinson (1957) recognized, are multidimensional. This need not, in itself, present a difficulty since multidimensional space can be simplified to one dimension for the purposes of modeling. Nor is it a problem that the components of niche space (temperature, pH, food availability, etc.) will vary from one community to another. However, as Tokeshi (1993) notes, the distinction between the fundamental and the realized niche (*sensu* Hutchinson) is rarely made in investigations of biological diversity. Indeed, as he observes, most niche apportionment models are framed in terms of the fundamental niche even though the relative abundances of species will be much more dependent on the magnitude of the realized niche. Since the relative abundance of species, usually measured as either number of individuals or biomass (see p. 138), is used as a surrogate of niche size when

testing the models, a potential difficulty arises. None the less, Tokeshi suggests that this problem will not be too serious if the models are viewed as pertaining to realized niches, or a combination of realized and fundamental niches, rather than simply to fundamental ones.

A further concern is that niche-based models are too simplistic to describe the biological world we know. For instance, a new species arriving in a community may affect the resources that a whole group of species depend on rather than invading the niche of an individual species. A classic, and topical example, is the impact that the invasive water hyacinth is having on the biodiversity of Lake Victoria.

There is another consequence of this preoccupation with the niche. Since their inception, species abundance distributions have been used to describe a variety of assemblages ranging from small, well-defined ensembles to large, heterogeneous groupings of species. Realized niches are shaped by ecological interactions within a community and the relative abundance of a species will reflect, to a greater or lesser extent, its success in dealing with competitors, predators, and parasites. If the assemblage under study represents a functional ecological unit, that is one where the component species interact with one another, then it is logically appropriate to apply a niche-based model to it. Tokeshi's (1993) view, that such models are most relevant to small ensembles of related species sharing similar resources, narrows the definition of assemblage further (see p. 14 for a discussion of the unit of study in investigations of ecological diversity). It also implies that competition is the most significant ecological interaction in these tightly defined domains.

The corollary of this is that the niche-based models may lose their application in larger assemblages spanning a variety of trophic levels, or where the species concerned no longer interact with one another, or where they are subject to a range of abiotic conditions. In such cases statistical models may be required. This is not to say that such statistical models are necessarily less valuable than the biological ones. A statistical model can provide an excellent description of the diversity of an assemblage and has many applications, for example in monitoring changes in community structure following a perturbation. Nor are biological models invariably inappropriate in species-rich assemblages. Tokeshi's (1996) power fraction model (see below) appears to have considerable application in such contexts.

Ecological and evolutionary processes

Biological models are mechanistic, that is they attempt to relate the way in which total niche space is divided amongst the species in an assemblage to the abundances of the species in question. Traditionally, niche apportionment models have assumed a process of **niche fragmentation** (Tokeshi 1990), that is the subdivision of already occupied niches. However, **niche filling** is another mechanism by which additional species can be accommodated. For example, a newly formed habitat such as an island or lake will provide empty niche space for colonizing species (MacArthur & Wilson 1967). As the diversity of an assemblage increases, the distinction between niche fragmentation and niche filling may blur. Moreover, evolutionary processes can mirror and reinforce ecological ones. Witness the >500 species of cichlid fish that have evolved in Lake Victoria in the last 100,000 years (Turner 1999; Verheyen *et al.* 2003). Although the distinction between, and relative importance of, niche filling and fragmentation warrants further investigation, Tokeshi (1999) points out that niche apportionment models can be applied to both processes.

Distinctions between deterministic and stochastic models

An important distinction needs to be made between deterministic and stochastic models. Deterministic models assume that N individuals will be distributed amongst the S species in the assemblage in a predetermined way. For example, the log series model will always assign 12.96 species to the smallest abundance class (of one individual) in an assemblage with 52 species and 663 individuals overall. The geometric series is the only deterministic niche apportionment model. Stochastic models, on the other hand, recognize that replicate communities structured according to the same set of rules will inevitably vary somewhat in terms of the relative abundances of species found there. This makes biological sense. For instance, 10 new islands, of identical size and distance from the mainland and formed at the same time, would be predicted, on the basis of MacArthur and Wilson's (1967) theory of island biogeography, to be colonized by similar numbers of species. None the less, the relative abundances of those species would undoubtedly differ from island to island. Stochastic models try to capture the random elements inherent in natural processes (see also Figure 2.18). Perhaps not surprisingly, they can be more challenging to fit than their deterministic counterparts. From a practical standpoint it is necessary to know whether a model is deterministic or stochastic to fit it to empirical data (see below).

The variety of niche-based models can seem bewildering. Different assumptions, in terms of the precise nature of niche apportionment, produce subtly different models. For example, MacArthur's broken stick assumes that total niche space is divided simultaneously, whereas niches in Tokeshi's MacArthur fraction model are partitioned sequentially—a more realistic ecological and evolutionary scenario. However, both models predict the same species abundance distribution. The require-

ment of replicated data adds further complexity to the testing of stochastic models (see below). These complications may explain why niche apportionment models, and in particular Tokeshi's refinements of them, have received relatively little attention over the past decade. Nevertheless, these models are an important ecological tool and their potential in elucidating empirical patterns of diversity has only just begun to be realized.

From a practical perspective it may be helpful to think of niche apportionment models as being arranged along a continuum from low to high evenness. The geometric series and dominance pre-emption models represent assemblages in which evenness is very low, that is ones in which a few dominant species control most of the resources. The random assortment, random fraction, power fraction, MacArthur fraction, and dominance decay models apply to progressively more even assemblages (Tokeshi 1999; see also p. 51 below).

Geometric series

Visualize a situation in which the dominant species "pre-empts" proportion k of some limiting resource, the second most dominant species pre-empting the same proportion k of the remainder, the third species taking k of what is left and so on until all species (S) have been accommodated. If this assumption is fulfilled and if the abundances of the species are proportional to the amount of the resource they utilize, the resulting pattern of species abundances will follow the geometric series (or niche pre-emption hypothesis) (see Figure 2.3). In a geometric series the abundances of species ranked from the most to least abundant will be (Motomura 1932; May 1975):

$$n_i = NC_k k(1-k)^{i-1}$$

Where n_i = the total number of individuals in the ith species; N = the total number of individuals; k = the proportion of the remaining niche space occupied by each successively colonizing species (k is a constant); and $C_k = [1-(1-k)^S]^{-1}$ and is a constant that insures that $\Sigma n_i = N$.

Because the ratio of the abundance of each species to the abundance of its predecessor is constant through the ranked list of species, the series will appear as a straight line when plotted on a log abundance/species rank graph (see Figure 2.4). Drawing this type of plot is one way of deciding whether a data set is consistent with the geometric series. Worked example 4 explains how to fit the series as well as offering some suggestions about what to do if the points do not all fall on a straight line. A full mathematical treatment of the geometric series can be found in May (1975), who also presents the species abundance distribution corresponding to

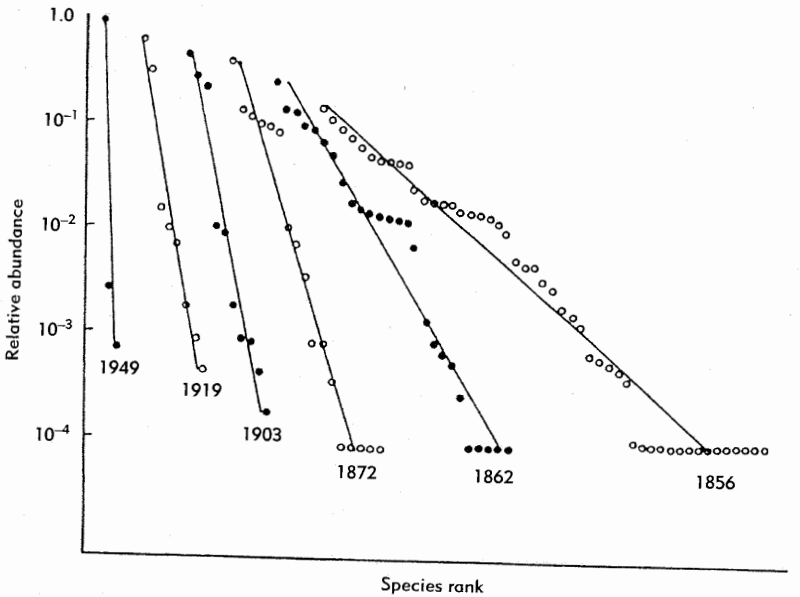

Figure 2.16 Changes in the relative abundance of plant species in the Rothamsted Park Grass Experiment over time. The grass has been subjected to continuous application of nitrogen fertilizer since 1856. (Redrawn with permission from Tokeshi 1993.)

the rank/abundance series. As noted above (see also Tokeshi 1993), the geometric series is the only deterministic member of the group of niche-based models.

Field data have shown that the geometric series pattern of species abundance is found primarily in species-poor (and often harsh) environments, or in the very early stages of a succession (Whittaker 1965, 1972). As succession proceeds, or as conditions ameliorate, other models may provide a better description of the community. However, Tokeshi (1993) observes that it is possible to relax the need for a very tight association between the data and the model—in the way that would be required if one were to formally fit the series—and to view it primarily as a descriptive statistic. This means that the series can be fitted approximately (using linear regression) and the slope of the regression adopted as a measure of evenness and used to track changes in community structure. (This approach was independently suggested by Nee *et al.* (1992); see also Chapter 4 for an assessment of its utility as an evenness measure.) Tokeshi (1993) illustrates this method in the context of the classic Park Grass Experiment at Rothamsted (Brenchley 1958) and shows how effective it is in encapsulating changes in diversity (Figure 2.16). This method also overcomes the problem, so often encountered in comparative stud-

ies of diversity, where no single model fits a range of communities.[4] It obviates the need to estimate goodness of fit, a procedure fraught with difficulties (see p. 43) or to make comparisons between deterministic models, such as the geometric series, and stochastic ones, such as the broken stick.

MacArthur's broken stick model

The broken stick model, sometimes known as the random niche boundary hypothesis, was proposed by MacArthur in 1957. He likened the subdivision of niche space within a community to a stick broken randomly and simultaneously into S pieces. It is a very uniform distribution—perhaps the most uniform ever found in natural communities. A major criticism of the model is that it may be derived from more than one hypothesis (Pielou 1975). Nevertheless, since the existence of a broken stick distribution provides evidence that an important ecological factor is being shared more or less evenly between species, it has served to shape ecological thinking on the processes that might underlie the patterns observed (May 1975). The model may also be viewed as representing a group of S species of equal competitive ability jostling for niche space (Tokeshi 1993).

Like the geometric series the broken stick model is conventionally written in terms of rank order abundance. The number of individuals in the ith most important species (n_i) is obtained from the term (May 1975):

$$n_i = \frac{N_T}{S} \sum_{n=i}^{S} \frac{1}{n}$$

Where n_i = the abundance of the ith species; N = the total number of individuals; and S = the total number of species.

Wilson (1991) provides a method of fitting a broken stick model to rank/abundance data. Drozd and Novotny's (2000) program can be used to estimate the species abundances associated with the broken stick.

May (1975), after Webb (1974), expresses the model in the form of a conventional species abundance distribution:

$$S(n) = [S(S-1)/N] \cdot (1 - n/N)^{S-2}$$

The broken stick, like other niche apportionment models, predicts the average species abundance distribution. Pielou (1975) likens this to drawing a card from a well-shuffled deck. If the cards are assigned values ranging from 1 for an ace and 13 for a king, the average denomination of a randomly chosen card will be 7. However, a single draw is no more likely to produce a 7 than any other card. It is only after many repeated draws that the "expected" average of 7 will be obtained. In a similar fashion the equation on p. 50 is predicting the distribution of species abundances across a number of replicate assemblages.

It is therefore inappropriate to fit the model to a single data set, even, as I suggested previously (Magurran 1988) as a statistical as opposed to a biological descriptor. Indeed, the broken stick can be tricky to fit to empirical data (Tokeshi 1993). There are, none the less, a few tests of the broken stick in the literature. Wilson *et al.* (1996), for example, found that the evenness of species abundances in plant assemblages increased over time. This was reflected in a relatively better fit by the broken stick model to older assemblages, though the fit was still poor in absolute terms.

4 Likewise, it is often advocated that a parameter of the log series model, α, can be used as a measure of diversity, even if the log series model does not perfectly describe the assemblage in question (Kempton & Taylor 1976; see also Chapter 4).

Table 2.2 A summary of Tokeshi's models.

Model	Selection of niche for division
Dominance pre-emption	Smallest niche always chosen
Random fraction	Niche chosen at random
Power fraction	Niche chosen at weighted random
MacArthur fraction	Probability that niche is chosen is proportional to its size
Dominance decay	Largest niche always chosen
Random assortment	No conventional niche apportionment assumed
Composite model	Niches of the abundant species are apportioned according to the dominance pre-emption, random/power fraction, MacArthur fraction, or dominance decay models while niches of rare species follow the random assortment model

Tokeshi's models

Tokeshi (1990, 1996) developed several new niche apportionment models: the dominance pre-emption, random fraction, power fraction, MacArthur fraction, and dominance decay models (Table 2.2). Each of these makes the assumption that the fraction of niche space occupied by a species is proportional to its abundance. Niche space is sequentially divided amongst the species as they join the assemblage. In all cases the models assume that the target niche—the one selected for division—is divided at random. The differences between the models lie in the way in which the target niche is selected. And the larger this niche is, relative

to the others in the assemblage, the more even the resulting distribution of species abundances will be. Evenness is thus lowest in the dominance pre-emption model, and increases progressively with the random fraction, power fraction, MacArthur fraction, and dominance decay models. Tokeshi contrasted these niche apportionment models with two other scenarios. The random assortment model represents a random collection of niches of arbitrary sizes (Tokeshi 1990). Finally, the composite model assumes that more than one rule is required to account for the structure of the assemblage—the abundances of common species are set by niche apportionment whereas the abundances of the rare ones are determined by random assortment. These models are reviewed below. In some cases the distinctions between them are quite subtle and several are probably impossible to separate in the field. I therefore draw the reader's attention to the random fraction model and (the related) power fraction models as these have, in my opinion, the greatest application to empirical data. The other models will, I suspect, be used primarily in theoretical analyses of niche apportionment, or to create benchmark assemblages of high or low evenness against which natural assemblages can be compared.

Dominance pre-emption model

Tokeshi's dominance pre-emption model assumes that each species in turn pre-empts more than half of the remaining niche space and is thus dominant over all remaining species combined (Tokeshi 1990). The proportion of available niche space occupied by each successively colonizing species is randomly assigned between 0.5 and 1. This model is conceptually similar to the geometric series and will produce, over many replications, a similar distribution of species abundances when $k = 0.75$ (see the discussion of geometric series above). Although initially formulated to describe a process of niche filling (Tokeshi 1990), this model can also be applied to niche fragmentation (Tokeshi 1993, 1999). In the latter case new colonists subdivide the niche of the least abundant species. The geometric series and dominance pre-emption model depict the least even communities likely to be found in nature. Figure 2.17 illustrates the pattern of relative abundance produced by this and some of Tokeshi's other models.

Random fraction

Tokeshi's random fraction model is an innovative model which has the potential for wide application. It was conceived (Tokeshi 1990) as a sequential breakage model in which the available niche space is initially divided, at random, into two pieces. One of these pieces is then selected at random for the second division and this process continues until all

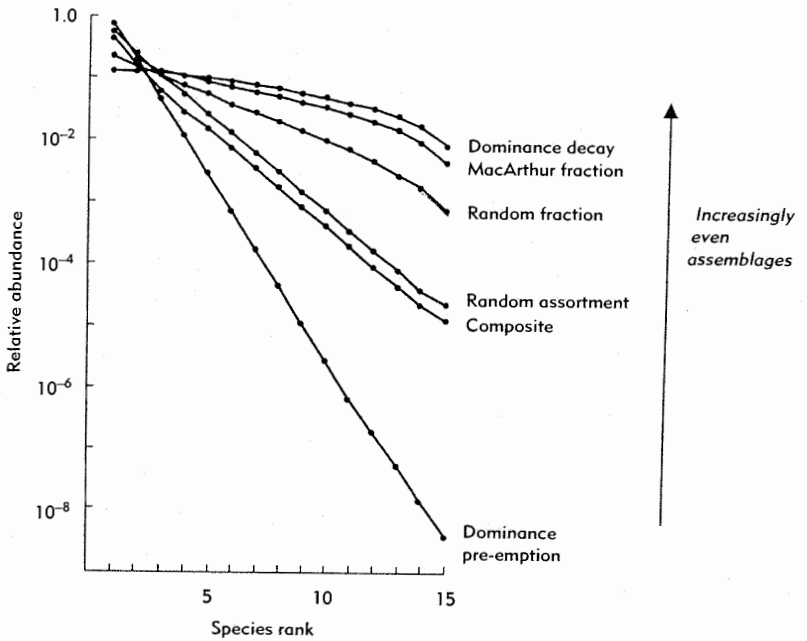

Figure 2.17 Pattern of relative abundance exhibited by a selection of Tokeshi's niche apportionment models. (Redrawn with permission from Tokeshi 1999.)

species are accommodated (Figure 2.18). The model represents a situation in which a new colonist competes for the niche of a species already in the community, and takes over a random proportion of this previously existing niche. Tokeshi (1999) subsequently pointed out that the model can be extended to cover speciation events. This presupposes that the probability of speciation is independent of the size of a species' niche. There are conflicting opinions on how the abundance of a species, or indeed the extent its range (both measures being surrogates for niche size), affects the likelihood of speciation. Intuitively it might seem that species with large range sizes are more likely to speciate than those with small ones. Darwin (1859) was the first to make this prediction and, as Gaston and Chown (1999) note, the idea continues to attract support (see, for example, Rosenzweig 1995; Tokeshi 1999). This is because larger ranges appear to offer more opportunities for fragmentation or subdivision by a barrier, thus facilitating allopatric speciation. However, it has recently been argued (Gaston & Chown 1999) that it is in fact the species with small to intermediate range sizes that are more likely to speciate. Widely distributed species have good dispersal abilities (Mayr 1963) which enhance gene flow (Rice & Hostert 1993), whereas species

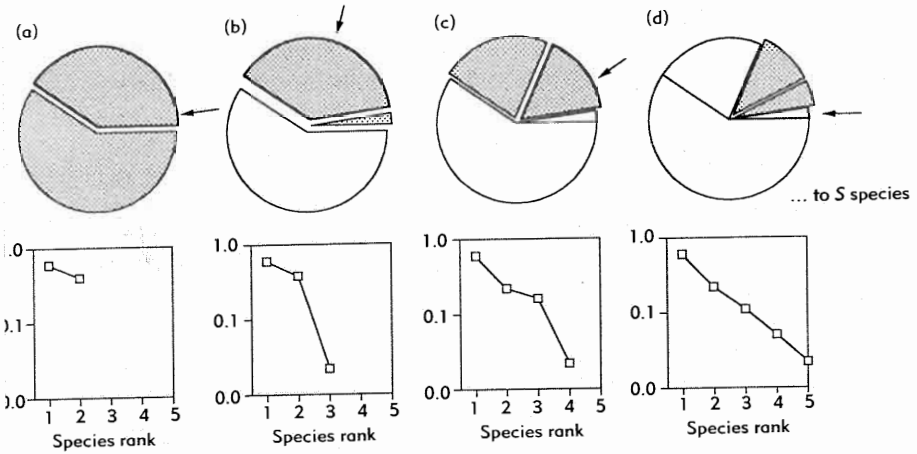

Figure 2.18 Illustration of Tokeshi's random fraction model. In this model niche space (represented as a pie digram) is initially split at random into two pieces to form (a). (Niches that have been formed by the split are indicated by stippling.) One of these pieces (outlined in bold) is chosen at random and then split at random (indicated by an arrow) to form (b). The process is repeated (c and d) until S species have been accommodated. Every time the model is rerun a slightly different pattern of niche allocation emerges. The one illustrated here represents the average result (for $S = 5$ species) after 250 runs. Rank/abundance plots illustrate the relative species abundances produced following each successive division.

with poor dispersal abilities will tend to form patchy populations and thus have higher speciation rates (Gaston & Chown 1999). Although the random fraction model is conceptually simple, Tokeshi (1990) and Fesl (2002) found that it provided a good fit for a small community of freshwater chironomids.

Drozd and Novotny (2000) have created a freeware Microsoft Excel-based program[5] that can be used to model the distribution of species abundances associated with the random fraction, power fraction, broken stick, and other niche division processes.

Power fraction model

As noted above, the majority of niche apportionment models are logically appropriate for small assemblages of related and/or ecologically interacting species. Tokeshi's power fraction model (1996) is an exception that is applicable to species-rich assemblages. Like the random fraction model it envisages that niche space is initially subdivided at random.

5 http://www.entu.cas.cz/png/PowerNiche/.

Box 2.1 **The power fraction model**

In Tokeshi's **power fraction** model, the probability that a niche will be targeted by an invading species is a function of its size when that size has been raised to the power K. K ranges between 0 and 1. Three scenarios are illustrated below (Figure B2.1).

Imagine an assemblage of three species which have abundances of 50, 25, and 25 units. Niche size is assumed to reflect the abundance of a species. Abundances (x) here are expressed as percentages but they could equally well be represented as proportions. These abundances are first raised to the power K. When $K = 0$, the abundance of each of the species becomes 1. This means that every species has an equal probability of being selected for niche subdivision. In this scenario, the power fraction and the random fraction are identical, since the (random) choice of a niche for subdivision is made without regard to the size of that niche. A value of $K = 0.5$, on the other hand, is equivalent to a square root transformation of abundance. In other words, species A is now 1.41 times as likely to be selected as either species B or C. In the final scenario, $K = 1$ and the initial abundances are unaffected and the niche of species A has double the probability of being split as either B or C. This is the same as the MacArthur fraction model.

The randomization process is illustrated for scenario 2 ($K = 0.5$) in Figure B2.1. The transformed abundances are now presented as cumulative precentages and a random number (between 0 and 100) drawn. If this random number happened to be 48, species B would be chosen (B occupies the slot of ≥41.4% and ≤70.7% in the cumulative abundance distribution). B's niche is then divided at random into two pieces. These new niches will have a summed abundance of 25 units since it is the true (untransformed) niche space that is being divided – the weighting simply changes the probability with which a niche of a particular size is chosen. This continues until the assemblage reaches its designated richness. Since each run of the model produces a slightly different outcome the whole process is repeated a large number of times so that the mean pattern of relative abundance is generated. This can then be compared with empirical data.

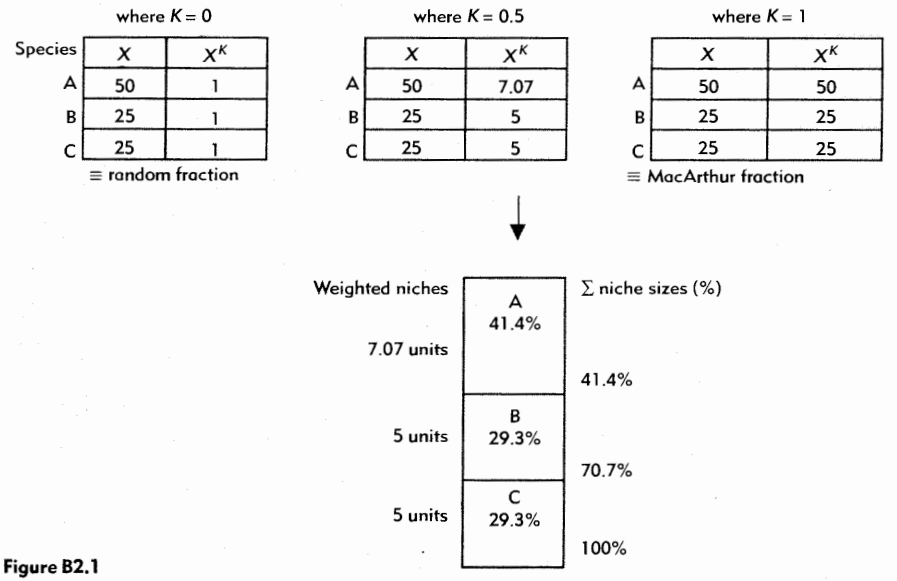

Figure B2.1

One of the resulting niches is then selected and again split at random. The process continues until all species have been accounted for. However, the name of the model, power fraction, highlights a subtle difference between it and the random fraction model. In the random fraction model the choice of niche to be split is strictly random. By contrast, in the power fraction model, the probability that a niche will be split is positively, though rather weakly, related to its size (x) through a power function K (that is x^K where K ranges from 0 to 1). The closer K approaches 1, the more likely it is that the largest niche will be selected for fragmentation. Indeed, when $K = 1$ the power fraction model resembles the MacArthur fraction model (in which larger niches have a greater probability of fragmenting). On the other hand when $K = 0$, a completely random choice of niche fragment is restored, and the model corresponds to the random fraction. (See Box 2.1 for an illustration of the power fraction model.)

Tokeshi (1996) showed that when the parameter K was set at 0.05 the power fraction model provided a good description of a range of species-rich assemblages. In fact virtually all the assemblages he investigated could be accounted for by a value of $K \leq 0.2$. He interprets this finding as evidence that larger niches have a slightly greater chance of being fragmented. Such fragmentation could occur either ecologically (when a new species colonizes an assemblage) or evolutionarily (when speciation takes place) (Gaston & Chown 1999).

As already observed, a reduction in the value of K increases the resemblance between the power fraction and random fraction models. Since K is apparently low in natural assemblages there may be many instances in which both models describe observed patterns of species abundance equally well (Tokeshi 1999).

One of the frustrations of diversity measurement has always been the necessary recourse to different models to account for contrasting patterns of species abundance. The fact that the value of the parameter K can be adjusted to depict different forms of niche apportionment means that a more integrated approach to the investigation of ecological diversity may at last be possible. This benefit is enhanced by the ability of the power fraction model to account for patterns of species abundance in large as well as small assemblages and at scales ranging from ensemble to geographic region (Tokeshi 1999). This flexibility can be viewed as a weakness rather than a strength (Gaston & Blackburn 2000).

MacArthur fraction model

One longstanding concern about the broken stick model is the unrealistic manner in which niches are split simultaneously. Tokeshi (1990, 1993) thus recast the process of niche fragmentation in a sequential, and therefore ecologically (and evolutionarily) more plausible, form. The

emphasis on sequential niche division also highlights the relationship between this model and other niche apportionment models. Both the MacArthur fraction and the broken stick models lead to the same result, in terms of the predicted species abundance distribution. This acts as a useful reminder that observation of a given pattern of species abundance does not necessarily validate the precise mechanisms assumed by a model predicting the same pattern. Further investigation is always warranted.

In the MacArthur fraction model the probability of a niche being fragmented is related to its size. Thus, larger niches are more likely to be subdivided by an invading species or through speciation. This process generates a very uniform distribution of species abundances and is only plausible in small communities of taxonomically related species. As already noted, the MacArthur fraction is a special case of the power fraction model, albeit one unlikely to pertain in species-rich assemblages.

Dominance decay model

An even more uniform pattern of species abundance is envisaged by Tokeshi's dominance decay model. In it the largest niche is invariably split. The sizes of the resulting fragments are chosen at random. (If the largest niche was always split in a fixed way this model would be the inverse of the geometric series and thus deterministic. Since the way in which the largest niche is split is decided randomly the model is stochastic, and therefore the mirror image of the dominance pre-emption model.) To date there are no empirical data indicating that communities as predicted by Tokeshi's dominance decay model can be found in nature. This may, of course, be because insufficient investigations have been conducted or because such an even distribution is genuinely not achievable under natural conditions. In any case the model performs the useful role of setting the upper level of evenness that might potentially be achieved by a niche apportionment process.

Random assortment model

Tokeshi realized that there may be situations where the abundances of species in a community vary independently of one another. This might arise if there is no relationship, or only a very weak one, between niche apportionment and species abundances, or if the community is in a state of flux, perhaps because it is subject to major environmental changes, and competition is not setting the limits on species abundances. Tokeshi (1993) notes that this model behaves as a stochastic analog of the geometric series model in which $k = 0.5$, and that it is similar in spirit to Caswell's (1976) neutral model (see below), which also assumes that the abundances of different species are independent of one another.

Composite model

The preceding models have each assumed that niche apportionment can be explained by a single rule. This may represent an oversimplification since two or more processes could equally well be involved. Tokeshi (1990) thus formulated his composite model. It assumes that competition is more likely to occur amongst abundant species and that these would therefore divide available niche space according to one of the niche apportionment models—dominance pre-emption, random/power fraction, MacArthur fraction, or dominance decay. The remaining rare species might be predicted to achieve their niches on the basis of random assortment. One potential complication is knowing where to set the boundary between the more abundant and less abundant species. (Gaston's (1994) quartile criterion of rarity (reviewed below) is one solution.) Another is deciding which niche apportionment scenarios to test. It is also possible to extend the model to accommodate more than two processes of niche subdivision (Tokeshi 1999). The composite model has not yet been comprehensively explored but its attempt to encapsulate ecological realism should prompt further investigation.

Hughes' dynamic model

Hughes' (1984, 1986) concern about the log normal model led him to devise his own dynamic model. It invokes competition as the structuring mechanism and was developed to explain the patterns of species abundance that characteristically arise in marine benthic communities. These assemblages often have more abundant species than predicted by the log series distribution but too few rare species to produce the mode that defines the log normal distribution. By visually inspecting rank/abundance plots from 222 animal and plant communities, Hughes concluded that his dynamics model predicted species abundance patterns more effectively than either the log normal or log series models. Barange and Campos (1991), however, preferred the Zipf–Mandelbrot model and felt it to be more appropriate in the light of the hierarchical organization of natural systems. Hubbell's (2001) neutral model (discussed below) makes a number of parallel assumptions. Both approaches, for example, incorporate birth and death processes. However, Hughes' model is more complex and specific than Hubbell's and to date has received relatively little attention.

Other approaches

Caswell's neutral model

Caswell's (1976) neutral model is rightly celebrated for its innovative approach to the analysis of community structure. In essence the model asks what the species abundance patterns in a community would be if all biological interactions were removed. Intriguingly, both species richness and evenness in real world communities tend to be lower than in the neutral landscape of Caswell's model. The deviation statistic, V, can be used to compare observed diversity (H') with the predicted neutral diversity ($E(H')$).

$$V = \frac{[H' - E(H')]}{SD(H')}$$

(H' is the Shannon diversity index. It is examined in detail in Chapter 4.) Values of $V > 2$ or $V < -2$ denote a significant departure from neutrality (Clarke & Warwick 2001a). Goldman and Lambshead (1989) provide a computer program for calculating V; this is implemented in PRIMER.[6] Although V is sometimes treated as a measure of environmental stress (Platt & Lambshead 1985; Lambshead & Platt 1988) it needs to be applied with caution. Given the complex relationships between richness and evenness in nature, V is probably only useful as a measure of disturbance when data from control unperturbed assemblages are available as a benchmark. Other more promising methods of assessing environmental stress are explored in Chapter 4. Moreover, Hayek and Buzas (1997) note that for reasonably large values of S and N the expected values of H' generated by the neutral model resemble those predicted by the log series model. The congruence in the outcome of different models has been noted already in this chapter and provides a further reminder that the biological interpretation of results is not always straightforward.

Hubbell's neutral theory of biodiversity and biogeography

Hubbell (2001) has developed an ambitious new neutral model that extends MacArthur and Wilson's equilibrium theory of island biogeography to account for regional as well as local patterns of biodiversity. In this approach metacommunities are defined as large-scale assemblages of trophically similar organisms that occur across evolutionary timescales. Each metacommunity is comprised of a set of local communities. Hubbell's model makes the assumption that communities are always saturated with individuals, and that there is a fixed relationship between N and area (A). No new individuals can be added through birth or immigration until N has been reduced by death. The relative abundance of each species in a local community is related to its abundance in the metacommunity; species abundances in the metacommunity are in turn shaped by speciation. Hubbell's theory can be encapsulated in a single di-

6 www.pml.ac.uk/primer/index.htm.

mensionless biodiversity number θ, which is equal to twice the speciation rate multiplied by the metacommunity size. It is this biodiversity number that predicts the relative abundance of species. If, for instance, metacommunity size (N) is held constant, while speciation rate is increased, more rare species will result. Alternatively, the speciation rate (v) may be held constant and the consequences of varying metacommunity size explored. Different models of speciation lead to different species abundance distributions in the metacommunity. For example, if point mutation, whereby new species arise as a single individual, is the dominant form of speciation, species abundances in the metacommunity will follow a log series distribution. In contrast, the random fission model of speciation, which produces two approximately equally abundant daughter species, results in a zero-sum multinomial distribution of species abundances. (See Hubbell 2001 for a full description.)

When immigration is unlimited the pattern of species abundance in a local community will be identical to that in the metacommunity (though species richness will be reduced as the spatial dimensions of the local community, and therefore the number of individuals it can support, will also be smaller). It will thus follow a log series or a zero-sum multinomial distribution, depending on the mode of speciation. Alternatively, if immigration is severely limited, perhaps because the local community is remote and there are barriers to dispersal, species abundances will resemble a log normal distribution. This is explained by the relationship between N and A. Extinctions must be compensated by increases in the abundance of existing species since there are few colonists to contribute new, but generally rarer, species to the community. At intermediate immigration rates the distribution of (logged) species abundances becomes skewed to the left—the pattern often observed in natural assemblages (Gaston & Blackburn 2000). Under such dispersal limitation the distribution of species abundances in local communities follows the zero-sum multinomial distribution, irrespective of the shape of the distribution in the metacommunity.

Hubbell's model is remarkable for its ability to account for a wide range of empirical species abundance distributions.[7] None the less the assumption of neutrality—defined by Hubbell (2001, p. 6) as the "per capita ecological equivalence of all individuals of all species in a tropically defined community"—runs against the grain for many ecologists familiar with the functional diversity of ecological systems (Brown 2001). It seems unlikely that the identity of the dominant species in a community is purely a matter of chance. Gaston and Blackburn (2000) also take issue with the assumption that assemblages are saturated with respect to the number of individuals they support. Magurran and Henderson (2003) have independently shown that dispersal limitation can account for the characteristic left skew in the species abundance distribution of local communities. In contrast to Hubbell's approach, biological interactions are assumed to play an important role. We use a mixture of the log series and log normal models to account for empirical patterns.

[7] McGill (2003), however, finds that the log normal distribution fits empirical data better than Hubbell's zero-sum multinomial.

Hubbell's model has already stimulated a great deal of interest and will undoubtedly give rise to many new studies. One complication is that simulations are required to estimate the fundamental biodiversity number and dispersal rate for empirical data sets. Hubbell (2001) provides an algorithm for computing the expected relative abundance distribution of a metacommunity assuming point mutation speciation. A fitting routine is promised for the zero-sum multinomial (see also McGill 2003).

Fitting niche apportionment models to empirical data

How does an investigator establish whether an assemblage conforms to one (or more) niche apportionment models? Clearly the best approach is to have an expectation of possible modes of niche subdivision based on an understanding of the ecology of the assemblage in question. For example, if competition is known to be important it is logical to apply a model that emphasizes this process. Beyond this, the size of an assemblage and the degree of evenness in the observed pattern of species abundance may indicate a starting point.

In statistical (and deterministic) models, as noted earlier, the usual procedure is to compare the observed pattern of species abundance with the patterns predicted by a particular model. Stochastic models present a different challenge. Rather than assuming (as deterministic models do) that N individuals are distributed amongst S species in a fixed manner, stochastic models recognize that random variation in the natural world will produce a slightly different outcome every time a community is assembled according to a given set of rules. As a consequence the investigator needs to be able to predict the mean abundances of each of the species in an assemblage, and to assign confidence intervals to these mean values. This necessitates a simulation procedure in which the community is repeatedly reconstructed. Strictly speaking, comparisons between these expected abundances and a real assemblage should only be made when replicated observations of the latter are used (Tokeshi 1990, 1993). This clearly places greater demands on the investigation, particularly if Tokeshi's (1993) advice to take more than 10 samples per assemblage (over space or time) is followed. In fact, since studies of niche apportionment tend to be small scale and intensive this requirement may not be as onerous as it initially appears. Furthermore, there are good reasons why replication should become standard practice in investigations of diversity. Replication means that variation in diversity, over

space and time, is amenable to statistical analysis (Chapter 4) and that estimates of total species richness are feasible (Chapter 3).

Tokeshi (1990) pioneered a new way of testing these stochastic models (see also Worked example 5). To summarize, $n \geq 10$ samples are taken. Species (S) are ranked from most abundant to least abundant. The mean abundance of the most abundant species ($x_{i=1}$) is calculated. This is repeated for the next most abundant species ($x_{i=2}$) and so on until the least abundant species ($x_{i=S}$) has been included. (In most cases, particularly those where the processes underlying niche fragmentation are of primary interest, it is not necessary to know the identities of the species in each replicate and the mean value of $x_{i=1}$ may be calculated regardless of the actual taxonomic species involved. In certain other circumstances, however, it may be important to know which species is which; see Tokeshi (1999) for a discussion.) These mean abundances constitute the observed distribution. The expected abundances are then estimated for an assemblage of the same number of species (S). To do this a model is chosen and then simulated a large number of times (say $N = 1{,}000$) using S species. (The randomness built into the models means that each simulation will lead to a slightly different outcome.) The mean (μ_i) and standard deviation (σ_i) of the abundance of each rank, $i = 1$ to $i = S$, are calculated. This allows the user to assign confidence limits to the expected abundance of each rank. These confidence limits are set in the usual way, with the important consideration that the sample size is n (that is the number of replicated samples of the assemblage) rather than N (the number of times the model was simulated).

$$R(x_i) = \mu_i \pm r\sigma_i/\sqrt{n}$$

where r defines the breadth of the confidence limit. It is 1.96 for a 95% limit and 1.65 for a 90% limit. If the mean observed abundances fall within the confidence limits of the expected abundances (see Worked example 5), the model can be said to fit the assemblage. Comparison between the observed and expected distributions is simplified if abundances are treated as proportional, that is the sum of the abundances (x_i) across all S species is $\Sigma x_i = 1$. Graphic presentation of the result is further clarified if these proportional abundances are plotted on a $\log_{10}$ scale. An advantage of this simulation approach is that it makes subtle distinctions between the possible distributions and spares the user the frustration that often accompanies the application of deterministic models, several of which may apparently fit the same data set.

A potential problem arises if the number of species (S) varies from sample to sample (Tokeshi 1993). This should not matter if the variation is slight. Alternatively, the difficulty may be overcome by adjusting S to a common value, provided that such a value of S accounts for most of the abundance (>95%) in the replicated samples.

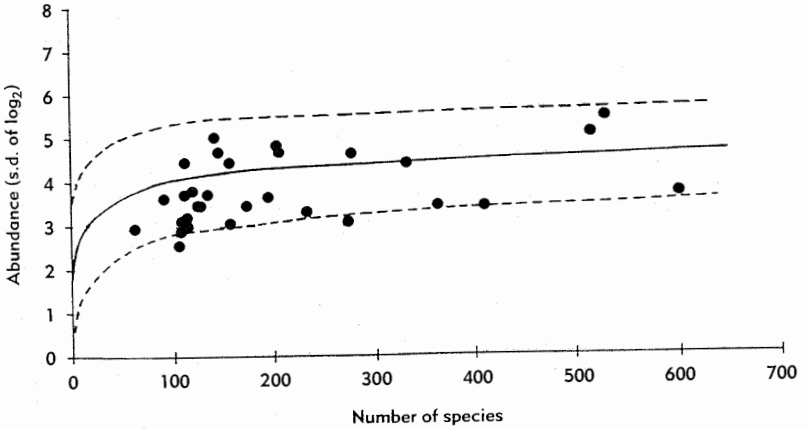

Figure 2.19 Testing the fit of a number of assemblages to a single model. Here a power fraction model with $k = 0.05$ is fitted to a series of species-rich assemblages. The solid line is the standard deviation of $\log_2$ abundance predicted by the model. Broken lines represent ±2 s.d. of this standard deviation. Theoretical values are derived from a large number of simulations. The graph reveals that miscellaneous assemblages conform to the power fraction model with $k = 0.05$. (Redrawn with permission from Tokeshi 1999.)

What happens if it has not been possible to replicate the sampling? Tokeshi (1999) notes that it may be legitimate to compare unreplicated ranked abundance data with the mean (±2 s.d. or ±95% confidence limits) simulated values of a model. Alternatively, the standard deviation of the $\log_2$ observed abundances of species can be plotted on a graph showing the mean (±2 s.d.) of the $\log_2$ expected abundances. This method is useful if the goal is to determine whether a number of species-rich assemblages share a common abundance distribution (Figure 2.19). Tokeshi also reminds us that unreplicated data are not appropriate for use with either the broken stick or MacArthur fraction models.

Bersier and Sugihara (1997) recognized that Tokeshi's method of relating stochastic species abundance models to field data represented an important first step but highlighted some shortcomings in the method. They observed that the test does not permit the rejection of data sets in which the variance is greater than that predicted by the model. Additionally, since the mean observed abundances of all species must lie within the expected confidence intervals, rich assemblages are more prone to rejection than species-poor ones. Distributions may be skewed, rendering symmetric confidence limits inappropriate and species ranks nonindependent. Bersier and Sugihara's (1997) solution was to propose a Monte Carlo test. One drawback to their approach is that it is computationally intensive. Cassey and King (2001) offer some important clarifications of Bersier and Sugihara's (1997) method and provide a test that

makes it computationally more efficient. Moreover, the algorithm that Cassey and King (2001) developed to implement the test, which is written for SAS, is freely available from the authors on request.

General recommendations on investigating patterns of species abundance

Previously, I (Magurran 1988) suggested that it would be informative to explore empirical data in relation to four species abundance models: the geometric series, log series, log normal, and broken stick distributions. These represent situations of increasing evenness. The expectation was that most assemblages would be described by a log normal distribution and that any departure from this pattern warranted further investigation. An obvious drawback of this approach is that it treated the models primarily as statistical descriptors of patterns rather than using them to infer biological processes. Interpretation could be impeded if the data were described by more than one model, or even by none at all.

Tokeshi's (1990, 1993, 1996, 1999) revaluation of species abundance distributions, his innovative niche apportionment models, and other advances in the field mean that this advice must now be updated.

1 It is important at the outset to know what the precise aims of the investigation are, and which hypothesis, if any, is being tested. This may sound obvious but it is a point that is often overlooked.

2 If the purpose of the investigation is to describe species abundance patterns, or quantify changes over time or space, for example through succession or following pollution, then replication of sampling, though strongly recommended, is not strictly necessary. However, it is essential that sampling be sufficiently thorough to reveal the true species abundance distribution (see Chapter 5 for a further discussion of sampling). On the other hand, should the study aim to relate the observed patterns to the ways in which the ecological niches have been carved up by the constituent species, replicated sampling increases the power of the investigation immeasurably.

3 The aims of the project will also help delineate the boundary of the assemblage under investigation. For example, an investigator interested in the biological basis of abundance patterns will often focus on a small assemblage of closely related organisms, since ecological interactions, particularly competition, are more likely to be discernible there (but see discussion of the power fraction model above). Tokeshi's niche apportionment models are fitted most easily to samples with the same species richness. Comparison of communities is also facilitated if they are equally speciose.

Studies involving the description of pattern are less constrained by size and can extend from small ensembles to large heterogeneous assemblages. However, comparisons between assemblages are again more straightforward, and probably also more meaningful, if species richness does not vary excessively.

4 In almost all investigations the most useful next step is to graph the data using a rank/abundance (Whittaker) plot. These plots are often the best way of illustrating differences in evenness and species richness. Wilson (1991) provides a method for fitting several key species abundance models to these plots (see also point 6 below).

5 If understanding niche apportionment is the goal, the investigator should fit one or more of Tokeshi's models. In some cases it may be useful to examine a range of models, but in others, particularly where it has been possible, from a priori knowledge of the system, to arrive at a hypothesis of niche apportionment, it will be obvious which model or models to test. Although there have been relatively few tests of Tokeshi's models to date, the random fraction model appears to be most generally applicable to small assemblages and the power fraction to larger ones (these models being, of course, closely related). It may not always be feasible, but ideally the next step would be to conduct experimental manipulations to confirm the niche apportionment mechanisms implied by the analysis.

6 Alternatively, when the objective is to describe the distribution of species abundances, an investigator has two options (which need not be mutually exclusive). The first is to examine the rank/abundance plot and compare communities using either k (the parameter of the geometric series) or the slope of a linear regression. This method neatly and intuitively encapsulates differences between the assemblages. It does not require the user to assess goodness of fit but simply equates the diversity of the assemblage with the slope of the regression. Analysis of covariance (ANCOVA) can be used to test for differences in slopes. The second option is to fit one or more models to the data. Depending on the outcome it may be possible to draw biologically interesting conclusions. For example, a log series distribution highlights the preponderance of rare species, and produces a robust diversity measure. A log normal distribution may be a useful gauge of pollution stress. The geometric series is often indicative of a species-poor assemblage and could imply that resources are being apportioned according to simple rules. The difficulty, of course, is that several different distributions may equally well describe the same data set. Moreover, the truncated log normal distribution is so versatile that it is a poor discriminator of communities. However, this problem can be largely overcome if the assemblages in question are reasonably speciose—with at least 30, but ideally 50 or more, species and where the presence of a mode in the distribution of (logged) species abundances indicates that a log normal distribution is plausible. Given the continuing debate, evidence that "natural" assemblages, as opposed to large heterogeneous collections of samples, follow a fully unveiled log normal distri-

bution would be an interesting, and undoubtedly publishable, result. The presence of log left-skew will also stimulate further investigation and analysis.

7 It may not be necessary to rely on species abundance distributions to distinguish between assemblages. Tokeshi (1993) notes that the Kolmogorov–Smirnov two-sample test can be used to determine whether two data sets have the same pattern of abundance. However, it is essential to make sure that the data have been collected in a standard way (see Worked example 3).

Rarity

This chapter has concentrated on species abundances. But if some species are common, then others, by definition, must be rare. Rarity, like abundance, is a relative concept; it will depend on the scale of the investigation and the manner in which the assemblage has been delineated. Different authors emphasize different aspects of abundance—endemicity, local population size, habitat specialization, and so on—when defining rarity. Gaston (1994) reviews these approaches and provides a unified definition of rarity. His method is particularly relevant to biodiversity measurement.

In the preceding discussion in this chapter, and in line with common practice, rare species were classed as those falling at the lower end of the distribution of species abundance. The boundary between rare species and the rest was not specified. Where this is desired, Gaston's (1994) advice is to place the cut-off point at the first quartile in terms of proportions of species. Thus, in an assemblage of 40 species, the 10 with the lowest abundance would be defined as rare (Figure 2.20). Likewise, the upper quartile can be used to identify common species. One potential drawback to this approach is that it de-emphasizes the proportion of low abundance species in an assemblage (Maina & Howe 2000). For instance, Robinson *et al.* (2000) noted that 33% of forest birds in Amazonian sites had densities of less than, or equal to, one pair per 100 ha, while Pitman *et al.* (1999) found that 88% of Amazonian tress had densities of less than one individual per hectare over a network of forest plots in Manu National Park, Peru. A small number of species will often account for 90% or more of the total abundance (see Figure 2.4 for an example) and one might legitimately consider the remaining majority to be rare. In addition, a rigid definition, such as the quartile criterion, may mask differences in the preponderance of rare species in different assemblages. When Robinson *et al.* (2000) examined the diversity of forest birds communities in Panama they found that only 17% of species were rare in contrast to 33% of species in Amazonia.

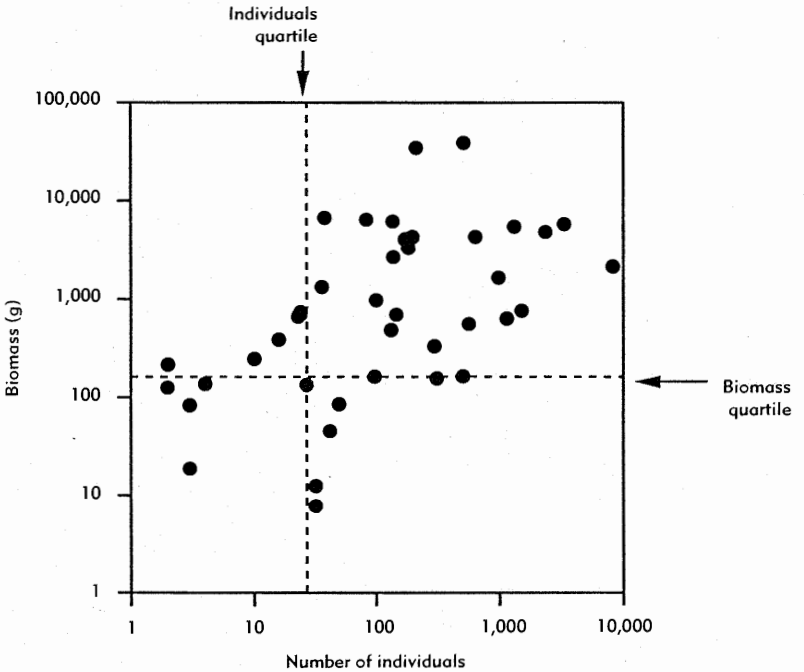

Figure 2.20 Rarity amongst freshwater fish in Trinidad and Tobago according to Gaston's quartile criterion. Fish abundance was measured in two ways – either as numbers of individuals or as biomass. Data were collected by Phillip (1998). The quartiles in the two distributions are shown as broken lines; fish species that fall to the left of the individuals line or below the biomass line are classified as rare. While there is substantial agreement about the nonrare species, only five (rather than the expected 10) out of the 41 species recorded are unequivocally rare according to both measures of abundance.

Abundance can be measured in different ways (see Chapter 5 for a full discussion). Different abundance measures may generate different sets of rare species; the degree of overlap will vary with taxon. In the freshwater fish example in Figure 2.20 there is some consistency between those species identified as rare on the basis of numbers of individuals, and those designated as rare using biomass data. As the variance in the biomass of individuals increases, agreement regarding the identities of rare species will diminish.

In addition, it is possible to apply **absolute** definitions of rarity. For instance, in an investigation of insect herbivores in New Guinea (Novotny & Basset 2000), rare species were classified as those represented by a single individual (otherwise known as a singleton). The same number of species from the upper end of the species abundance distribution were then defined as common, and the remainder designated "intermediate."

Singleton species are prevalent in insect assemblages and often constitute the largest abundance class. Indeed, this is why the log series distribution appears to have particular application in such contexts. Novotny and Basset (2000) found that when the assemblage was defined as the group of species associated with a single plant species, on average 45% of leaf-chewing and sap-sucking insects were singletons. A somewhat smaller proportion, 278 of the 1,050 species recorded, were represented by a single individual (unique singletons). While still an impressive total, this illustrates how even absolute definitions of rarity are contingent on the sampling universe and are in a sense relative. The investigation represented 950 person days of sampling. None the less, Novotny and Basset (2000) speculate that the unique singletons may belong to species that feed on plants other than those studied. The alternative explanation, that these species are genuinely sparsely distributed, would require them to persist at population densities below one individual per hectare of forest.

Longino *et al.* (2002) point out that sampling methodology can have a large impact on the perception of rarity. Their investigation of ants in Costa Rica employed eight different sampling methods. Rare species were defined as being locally unique (that is found in one sample only). The proportion of unique species varied from 0.13 to 0.47 (average 0.33) when data sets, collected using the different sampling techniques, were examined separately. However, when all data were combined the proportion of unique species dropped to 0.12 (51 out of 437). This may in part be a numerical effect—as more individual samples are collated the chances of identifying new species diminishes. But more importantly the different sampling methods insured that a wide range of ant niches were searched (see also Chapter 5). Longino *et al.* (2002) then went on to examine the status of their 51 locally unique species. The rarity of 20 of these species could be attributed to "edge effects," that is species likely to be abundant at the La Selva Biological Station but hard to sample, or species known to be common elsewhere but rare in this particular geographic locality. Only six species—the "global uniques"—were found in a single sample, and nowhere else on earth.

An "absolute" definition of rarity is also generally adopted when the abundance-based coverage estimator is used to deduce the species richness of an assemblage (Chazdon *et al.* 1998; Colwell 2000). In this case species having 10 or fewer species are typically defined as "rare." Chapter 3 provides more details.

As the scale of the investigation broadens, abundance data become harder to compile. With the exception of particularly well-studied taxa such as British birds, good abundance data are lacking for geographic regions. An alternative, and often more practical, approach is to look instead at the distribution of species' range sizes and use this as a surrogate of abundance. Gaston (1994) assesses various methods of quantifying

Table 2.3 The distribution of seven forms of rarity in the British flora using 160 species (after Rabinowitz *et al.* 1986, with permission).

Gegraphic distribution:	Wide		Narrow	
Habitat specificity:	**Broad**	**Restricted**	**Broad**	**Restricted**
Local population size: somewhere large	36%	44%	4%	9%
Local population size: everywhere small	1%	4%	0%	2%

Table 2.4 Seven forms of rarity amongst freshwater fish in Trinidad and Tobago using 40 species (after Phillip 1998, with permission).

Gegraphic distribution:	Wide		Narrow	
Habitat specificity:	**Broad**	**Restricted**	**Broad**	**Restricted**
Local population size: somewhere large	29%	13%	3%	16%
Local population size: everywhere small	13%	13%	0%	13%

range size. He also notes that species that are categorized as rare on the basis of abundance, will also generally be identified as rare on the basis of their range size.

There are exceptions, however. Some species inevitably fall within the quartile criterion of distribution but not abundance (and vice versa). Gaston (1994) resists the temptation to treat these as different forms of rarity. Other authors have argued that rarity is a multifaceted concept. Rabinowitz and her colleagues (Rabinowitz 1981; Rabinowitz *et al.* 1986), for example, argue that a species' rarity status is a function of three characteristics—geographic distribution, habitat specificity, and local population size. The authors (Rabinowitz *et al.* 1986) categorized British flora in this way and found that only some 36% of species were unequivocally common (Table 2.3). One category of rarity—narrow geographic distribution, broad habitat specificity, and an invariably small local population size—contained no species at all. A similar result was obtained when the freshwater fish in Trinidad and Tobago were classified in the same way (Phillip 1998) (Table 2.4), although when Thomas and Mallorie (1985) investigated patterns of rarity in butterflies of the Atlas Mountains in Morocco they did find a single species (out of 39) that matched these criteria. Evidently, this form of rarity is biologically hard to achieve.

This approach has considerable potential in conservation biology. Indeed, the International Union for Conservation of Nature and Natural Resources' "red data book" definition of rarity (Gaston 1994) incorporates the same variables:

Taxa with small world populations that are not at present *Endangered* or *Vulnerable* but are at risk. These taxa are usually localised within restricted geographical areas or habitats or are thinly scattered over a more extensive range.

However, in the context of biodiversity measurement, rarity is best viewed as a continuous, as opposed to a categorical, variable. This is because we are generally engaged in providing quantitative comparisons between assemblages and it is easier to achieve these if rarity is measured using a single metric. Categories of rarity are potentially less objective. They demand detailed information on the ecology of all the species in an assemblage. In addition, Rabinowitz's seven forms of rarity tend to be assigned at the level of the geographic region whereas many investigations of biological diversity take place at more local scales (but see also Chapter 6). Deciding where the rarity boundary falls on the continuum of rare to abundant species remains a difficult challenge. Gaston's (1994) quartile criterion provides a useful starting point but because assemblages vary in their evenness, and because the proportion of low abundance species will change according to the intensity of sampling and the scale of the investigation (the veil line again), it is not universally applicable. If the quartile method seems inappropriate, the usual alternative is to identify the species with the lowest abundance or incidence as rare—as Novotny and Basset (2000), Pitman *et al.* (1999), and Robinson *et al.* (2000) have done. The extent to which perceptions of rarity are governed by sample size will be considered further in Chapter 5 and the relationship between rarity and β diversity in Chapter 6.

This chapter has come full circle. It began by noting that assemblages can vary considerably in species richness but all are characterized by uneven distributions of abundance. The precise shape of the distribution of species abundances is of considerable fundamental and applied interest. It can shed light on niche apportionment in communities, help explain why particular levels of richness can be sustained, and monitor the effects of pollution stress (Chapter 5). Species abundance distributions may be used to estimate species richness—the topic of Chapter 3. Alternatively, statistics can be employed to summarize the diversity or evenness of an assemblage, but even though these are sometimes called "nonparametric" measures, their performance is mediated by the underlying pattern of species abundances. These statistics will be examined in Chapter 4.

Summary

1 Different plotting methods can be used to display the distribution of species abundances. Of these the rank/abundance plot (or Whittaker plot) and log(x) frequency distribution (or Preston plot) are most widely used.
2 Species abundance distributions can be classified as statistical or biological. Statistical models describe observed patterns whereas biological models attempt to explain them. Most statistical models are deterministic and most biological models stochastic.
3 The log series and log normal models are the widely used statistical models. There is still debate over whether the log normal is the expected distribution for large, unperturbed ecological assemblages. Empirical log normal distributions tend to log left-skewed. Reasons for this are explored.
4 Motomura's geometric series and MacArthur's broken stick model are two early examples of biological models. Tokeshi has proposed a series of new models reflecting different scenarios of niche apportionment. Of these the random fraction model and the related power fraction model appear to have greatest application to small and large assemblages, respectively. Methods of fitting niche apportionment models are discussed.
5 Null models of species abundance, including Caswell's and Hubbell's neutral models are reviewed.
6 General recommendations on investigating patterns of species abundance are given. The goals of an investigation will determine whether a biological or statistical model is appropriate. This in turn will guide the sampling strategy. Since species abundance distributions can be compared directly it may not be necessary to fit a model.
7 Rarity is discussed. Relative and absolute definitions of rarity are presented. From the perspective of biodiversity measurement, rarity should be treated as a continuous variable. Gaston's definition—that rare species are those that fall in the lower quartile of the species abundance distribution—provides a useful working definition.

chapter three

How many species?[1]

Describing the species abundance distribution of an assemblage is one thing; providing a synoptic measure of its diversity represents a rather different challenge. Considerable effort, particularly in the 1950s and 1960s, was devoted to finding a single measure that would perfectly encapsulate the diversity of the sample or community under study. This quest was ill fated from the beginning as biodiversity is not reducible to a single index (see Chapters 2 and 4 for further discussion of this point). Rather, it is necessary to decide which component of diversity one aspires to measure and then choose the index that performs this task most effectively.

At first sight, species richness seems to be the simplest, and most intuitively satisfying, measure of diversity. Species richness can be defined as the number of species of a given taxon in the chosen assemblage. Yet such simplicity is illusory. There is considerable debate about which species concept should be adopted. Most biologists adhere to Mayr's (1942) **biological species concept** (Coyne & Orr 1998; Futuyma 1998) but alternatives, for example the **phylogenetic species concept** (Cracraft 1989) and the **cohesion concept** (Templeton 1989) are also used. Added to this is the issue of **species discrimination** (Gaston 1996b). Taxonomists are often classified as "lumpers" or "splitters." The former approach has the result of decreasing species richness, the latter of inflating it. Greater investment in taxonomy may also boost estimates as new species are described and cryptic species distinguished—although the identification

1 After May (1990a).

of synonymies, where two or more scientific names have been applied to a single species, can actually reduce the total (Gaston & Mound 1993; Gaston *et al.* 1995). Inevitably, some groups are much less well known than others. Perhaps as many as 75% of species remain to be formally described (May 1990a). Morphotypes or morphospecies—taxa that are distinguishable on the basis of the morphology (Oliver & Beattie 1996a, 1996b)—provide a practical solution in circumstances where previously unrecorded or unidentifiable organisms are encountered (see Hammond 1994 for a more detailed discussion of this point). Morphospecies are usually treated as equivalent to species in richness estimates. Clearly, morphospecies will be more indispensable for some taxa than others: Lawton *et al.* (1998) conducted an inventory of a semideciduous humid forest in southern Cameroon in which over 90% of recorded soil nematodes—but no birds—had to be assigned to morphospecies. It is particularly important that morphospecies are classified and identified consistently when comparisons between localities are being made as inconsistencies can produce significant errors in richness estimates (Hammond 1994).

Sampling brings further complications. Even when species can be unambiguously identified it is rarely cost effective to record every species in an assemblage. If larger areas are examined more species will be revealed (Figure 3.1a). Estimates will increase as sites are explored more thoroughly, or surveyed over longer periods so that diurnal and seasonal activity rhythms are accounted for (Figure 3.1b). And, since assemblages, including isolated ones such as islands (Rose & Polis 2000), are not closed systems, the cumulative list of species will creep ever upwards as new colonists arrive (MacArthur & Wilson 1967; Holloway 1977; see also Chapter 5).

Effective sampling must also take heed of the underlying species abundance distribution and greater effort will be required in situations where evenness is low (Lande *et al.* 2000; Yoccoz *et al.* 2001). Imagine, for instance, that there are two assemblages, each with the same number of species and individuals, but whose species differ in their relative abundances. In the assemblage where all species are more or less equally common, sampling will soon provide an accurate estimate of its richness. On the other hand, samples taken from the assemblage where one species dominates and the others are rare will tend to underestimate richness (May 1975) (Figure 3.2). A further problem is detectability—not all species or individuals are equally easy to sample (Southwood & Henderson 2000) and this can be a potential source of error (Yoccoz *et al.* 2001). Methodological edge effects arise when the probability of species capture is not directly related to species abundance (Longino *et al.* 2002). With these caveats in mind this chapter considers methods of measuring species richness and evaluates their effectiveness.

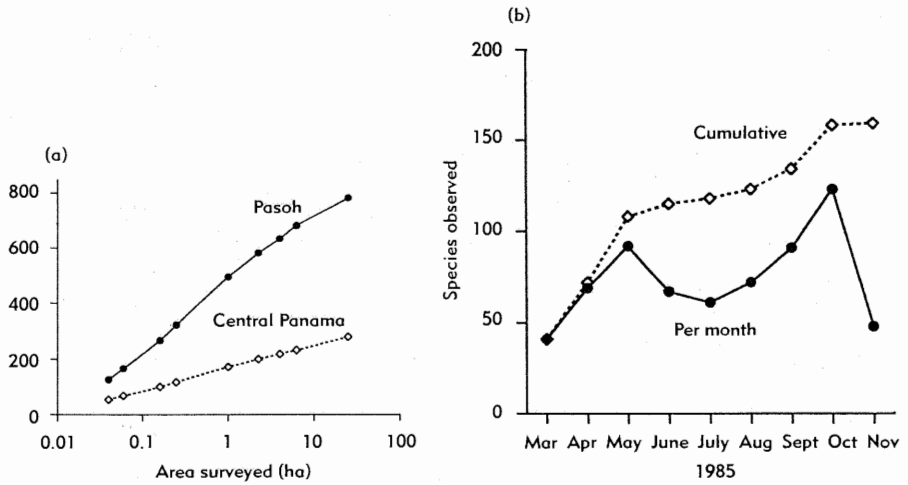

Figure 3.1 (a) Spatial effects and species richness. The graph illustrates the relationship between area surveyed and number of species recorded in a wet, old-growth forest in Malaysia (Pasoh) and a moist, old-growth forest in central Panama. Data relate to plants with stems ≥10 mm dbh (from Condit *et al.* 1996). (b) Temporal effects and species richness. The graph shows the number of bird species observed on the Isle of May (off Scotland's east coast) during 1985. Data are presented as the number of species per month, and cumulative total number of species recorded over the year. The influx of spring and autumn migrants in May and October, respectively, is clearly visible. (Data courtesy of Fife Nature.)

Measures of species richness

In circumstances where the fauna or flora are well known and not too speciose it may be possible to record, with a fair degree of accuracy, absolute species richness. In practice this usually means temperate and often terrestrial or freshwater assemblages of vertebrates, such as North American land mammals (Brown & Nicoletto 1991) and British freshwater fish (Maitland & Campbell 1992), or assemblages of higher plants, for example the vegetation of the Siskiyou Mountains in Oregon and California (Whittaker 1960). However, the real challenges in biodiversity assessment concern poorly documented (usually invertebrate) taxa in tropical or deep-sea assemblages. Here, high diversity combined with a relatively poorly documented biota and invariably limited funding, mean that an estimate of species richness is usually the best that can be achieved. Yet it is in these localities that the need for rapid, accurate, and cost-effective biodiversity inventories is most pressing. Lawton *et al.* (1998) estimated that up to 20% of the world's 7,000 systematists would

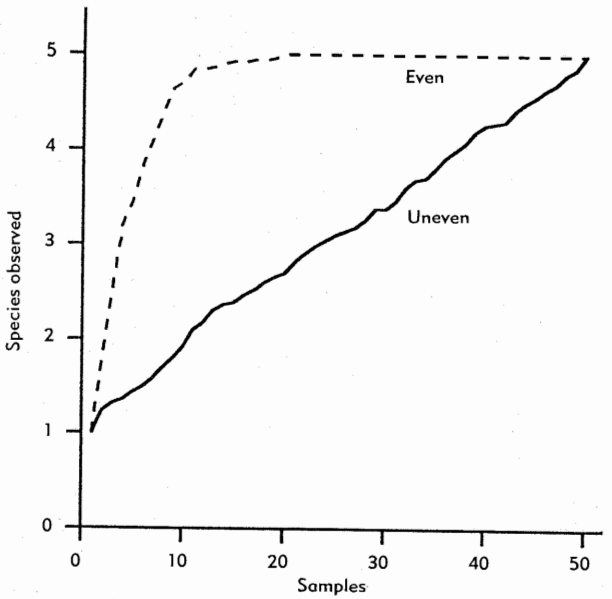

Figure 3.2 The effect of abundance distribution on richness estimation. Each assemblage consists of five species and 50 individuals. In the even assemblage each of these five species has 10 individuals; four of the species in the uneven assemblage are singletons while the remaining one has 46 individuals. The graph shows the estimate of species richness obtained by successively sampling (at random, and without replacement) an individual from each assemblage. This estimate is averaged over 50 randomizations. True species richness ($S = 5$) emerges much more quickly in the even assemblage than in the uneven one.

be required to produce an all-taxa biological inventory of a single "representative hectare" of forest in a reasonable time period. This calculation was based on their investigation of eight animal taxa in Cameroon where the equivalent of five "scientist years" was needed to sample, sort, and catalog the 2,000 species in the inventory. One consequence of the renewed interest in biological diversity in recent years is that ecologists have placed considerable emphasis on improved methods of estimating species richness. Fortunately, the news is good. Excellent progress has been made and there are now a number of robust and efficient estimators available.

There are two main methods of expressing estimates of species richness—as **numerical species richness**, which is the number of species per specified number of individuals or biomass, or **species density**, which is

the number of species per specified collection area or unit. Species density, for example the number of species per metre squared, is especially favored in botanical studies. The classic Park Grass Experiment, begun at Rothamsted in England well over a century ago (Lawes & Gilbert 1880; Lawes *et al.* 1882; Tilman 1982), typifies this approach. It continues to be used today, for example in investigations of the relationship between diversity and function (Hector *et al.* 1999). Numerical species richness, on the other hand, lends itself to animal taxa where individuals are readily identifiable and where the investigator has the option of continuing sampling until a certain minimum number of individuals are reached. For instance, micropaleontologists typically identify 300 individuals to species (Buzas 1990; Hayek & Buzas 1997; see also Chapter 5).

Gotelli and Colwell (2001) make the parallel distinction between **individual-based** assessment protocols, where individuals are sampled sequentially, and **sample-based** assessment protocols, in which sampling units, such as quadrats, are identified, and all the individuals that lie within them are enumerated. These sampling approaches have important implications for richness estimation (Gotelli & Colwell 2001; Longino *et al.* 2002; see also discussion in Chapter 5). Incidence (or occurrence) data offer a further method of deducing species richness. Incidences represent the number of sampling units in which a species is present. These sampling units can be grid squares, quadrats, pitfall traps, zooplankton hauls, or indeed anything that is collected in a systematic way. In effect incidences are species density data in another form.

A major problem with species richness estimates is their dependence on sampling effort (Gaston 1996b) (Figure 3.3). Sampling effort is rarely documented (Gaston 1996b). This presents a major problem to those who try to deduce the absolute richness of a taxonomic group or geographic area since the rate at which new species are recorded is an important variable in such estimates (Simon 1983; May 1990a; and see below). Lack of information on sampling effort also impedes the comparison of the richness of different localities (Gaston 1996b). None the less, the application of the new estimators—which encourage the user to explicitly state sampling methodology and size—may do much to remedy the situation.

Species richness indices

There are several simple species richness indices that attempt to compensate for sampling effects by dividing richness, S, the number of species recorded, by N, the total number of individuals in the sample. Two of the best known of these are Margalef's diversity index (Clifford & Stephenson 1975) D_{Mg}:

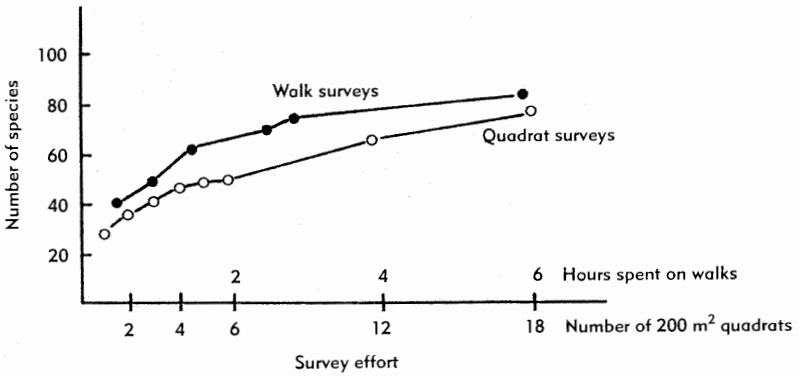

Figure 3.3 Observed richness is related to sampling intensity. This graph shows the relationship between the number of vascular plant species recorded and sampling effort, in walk surveys and quadrat surveys carried out in a broadleaved woodland in April. Each quadrat took approximately 45 min to complete. (Redrawn with kind permission of Kluwer Academic Publishers from fig. 3.3, Magurran 1988; after Kirby *et al.* 1986.)

$$D_{Mg} = \frac{(S-1)}{\ln N}$$

and Menhinick's index (Whittaker 1977) D_{Mn}:

$$D_{Mn} = \frac{S}{\sqrt{N}}$$

Ease of calculation is one great advantage of the Margalef and Menhinick indices. For instance, in a sample of 23 species of birds, represented by a total of 312 individuals, diversity would be estimated as $D_{Mg} = 3.83$ using Margalef's index and $D_{Mn} = 1.20$ using Menhinick's index. Convention dictates that the Margalef index is calculated using $S-1$ species and the Menhinick with S species.

Despite the attempt to correct for sample size, both measures remain strongly influenced by sampling effort. None the less they are intuitively meaningful indices and can play a useful role in investigations of biological diversity. The Margalef index is evaluated further in the following chapter.

Estimating species richness

As Colwell and Coddington (1994) and Chazdon *et al.* (1998) note, there are three approaches to estimating species richness from samples. The first of these depends on the extrapolation of species accumulation or

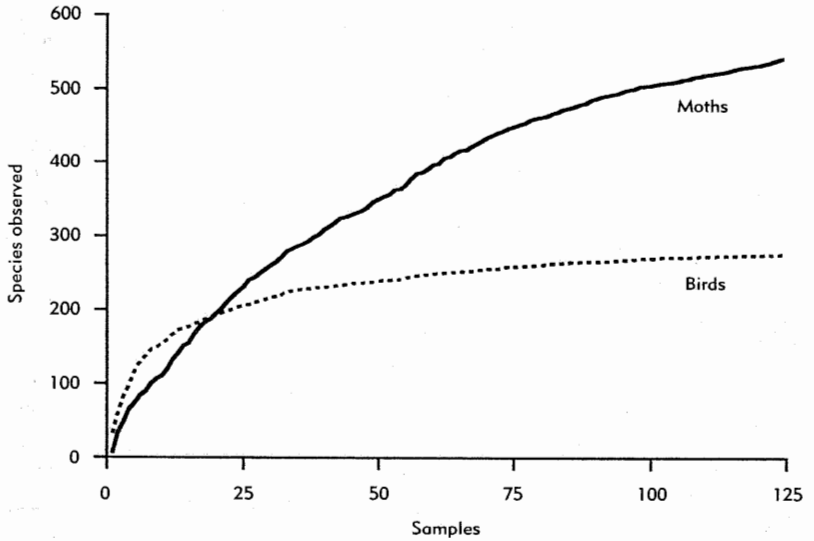

Figure 3.4 Species accumulation curves of moths and birds in Fife, Scotland. Graphs are based on species occurrence in 125, 5 × 5 km grid squares. Average species richness (based on 50 randomizations; see Colwell (2000)) is shown. The accumulation curve for birds—an extremely well-recorded group—is beginning to reach an asymptote. In contrast, the curve for moths, a much less intensively sampled taxon, shows no signs of leveling off. (Data courtesy of Fife Nature.)

species–area curves. Alternatively, it is possible to use the shape of the species abundance distribution to deduce total species richness. The final, and potentially most powerful, approach is to use a nonparametric estimator.

Species accumulation curves

When ecologists set out to determine the diversity of a locality they almost always take a series of samples. These might be quadrats, plankton hauls, light traps, or Malaise traps (Southwood & Henderson 2000). The rate at which new species are added to the inventory provides important clues about the species richness, and indeed the species abundance distribution, of the assemblage as a whole. Recently there has been renewed interest in species accumulation curves as a means of estimating species richness. Species accumulation curves, which are sometimes called collectors curves, plot the cumulative number of species recorded (S) as a function of sampling effort (n) (Colwell & Coddington 1994) (Figures 1.1 and 3.4). Effort can be the number of individuals collected, or a surrogate measure such as the cumulative number of samples or sampling time (Colwell & Coddington 1994). Species–area curves, widely used in botanical research (Arrhenius 1921; Goldsmith & Harrison 1976), are one form of species accumulation curves. It is important to note that there are two different forms of species–area curve—those that plot S versus A for different areas (such as islands) and those that examine increasingly larger parcels of the same region. Only the latter should be regarded as species accumulation curves since these depict the same universe sampled at different intensities.

The order in which samples (or individuals) are included in a species accumulation curve influences its overall shape. An especially speciose sample will, for example, have a much greater influence on the shape of the curve if it is encountered earlier rather than later in the sequence. A smooth curve can be produced by randomizing the procedure. To achieve this, samples (or individuals) are randomly added to the species accumulation curve and this procedure is repeated, say 50 times (Figure 3.4). The mean and standard deviation of species richness at each value of n can also be calculated. Gotelli and Colwell (2001) note that such resampling curves are closely related to rarefaction curves (Sanders 1968). Species accumulation curves are viewed as moving from left to right, as new species are added (Figure 3.5). They can be extrapolated to provide an estimate of the total richness of the assemblage. The following sections of this chapter explain how this is done. Rarefaction curves, in contrast, move from right to left. Here the goal is to deduce what the species richness of the assemblage would be if the sampling effort had been reduced by a specified amount. The purpose of rarefaction is to make direct comparisons amongst communities on the basis of number of individuals in the smallest sample. Rarefaction is discussed further in Chapter 5. Gotelli and Colwell (2001) note that Pielou's (1975) pooled quadrat method, devised to provide improved estimates of diversity indices, is analogous to the randomized (smoothed) species accumulation curve. Many investigators plot species accumulation curves using a linear scale on both axes. I have done this for the figures in this chapter. However Longino *et al.* (2002) recommend that the x axis should be log transformed since these semilog plots make it easier to distinguish asymptotic curves from logarithmic curves.

Species accumulation curves illustrate the rate at which new species are found. But unless sampling has been exhaustive, these curves do not directly reveal total species richness. More effort will uncover yet more species leading accumulation curves to creep ever upwards. One solution, first identified by Holdridge *et al.* (1971) (see Colwell & Coddington 1994) is to extrapolate from species accumulation curves to estimate total species richness. There are now a number of papers addressing the subject, though as yet no firm consensus on

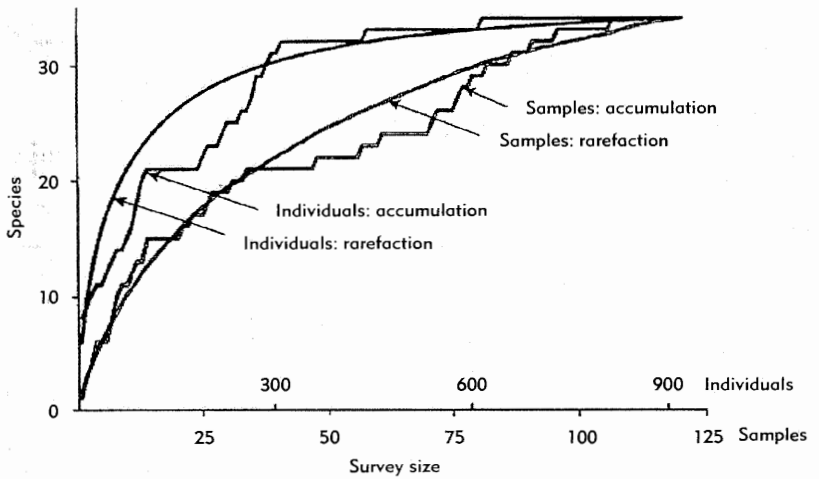

Figure 3.5 The distinction between species accumulation curves and rarefaction curves. Species accumulation curves are viewed as moving from left to right, rarefaction curves from right to left. A rarefaction curve can be regarded as the statistical expectation of the corresponding accumulation curve. Rarefaction curves represent the mean of repeated resampling of all pooled individuals or samples and are used to compare the species richness of two or more assemblages at a common lower abundance level. Species accumulation curves in contrast approach the total species richness of the assemblage. Rarefaction curves and species accumulation curves constructed using data on individuals typically lie above those based on sample data. This point is discussed further in the text. (Redrawn with permission from Gotelli & Cowell 2001.)

the best approach (Palmer 1991; Baltanás 1992; Soberón & Llorente 1993; Colwell & Coddington 1994; Chazdon *et al.* 1998; Keating & Quinn 1998).

Colwell and Coddington (1994, p. 106) argue that extrapolation becomes at least logically possible when a species accumulation curve represents a "uniform sampling process for a reasonably stable universe." This means, in effect, that samples should be taken in a systematic way, as opposed to the *ad hoc* collecting sometimes practiced by those wishing to maximize the number of new species recorded per unit time. Colwell and Coddington (1994) also advise that such extrapolations should be restricted to areas of reasonably homogenous habitat rather than being based on wide-ranging species–area curves, especially those that encompass large-scale biogeographic zones.

Functions used in this type of extrapolation may be either **asymptotic** or **nonasymptotic**. In both cases their most useful role is to allow the user to predict the increase in species richness for additional sampling effort rather than to estimate total species richness *per se*.

There are two main methods of generating an asymptotic curve. The first, based on the negative exponential model, was used by Holdridge *et al.* (1971) to compare the species richness of trees across climatic zones in Costa Rica, as well as by Soberón and Llorente (1993) and Miller and Wiegert (1989). The Michaelis–Menten equation, originally devised to model enzyme kinetics (Michaelis & Menten 1913) is the second. This approach has been used extensively in species richness estimation (de Caprariis *et al.* 1976; Clench 1979; Soberón & Llorente 1993; Colwell & Coddington 1994; Denslow 1995; Chazdon *et al.* 1998; Keating & Quinn 1998). In a novel application of the approach, Paxton (1998) estimated that 47 "sea monsters" (open-water marine fauna >2 m total length) remained to be discovered.

The usual form of the equation is:

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

where $S(n)$ = the number of species observed in n samples; $S_{\max}$ = the total number of species in the assemblage; and B = the sampling effort required to detect 50% of $S_{\max}$.

A variety of methods can be used to estimate the fitted constants, $S_{\max}$ and B, and their variances. Colwell and Coddington (1994) discuss the alternatives, advocate Raaijmakers' (1987) approach, and provide details of the methodology. When used with their rain forest seed bank data, the Michaelis–Menten approach underestimated species richness at small sample sizes. A subsequent study (Chazdon *et al.* 1998) found that it had a tendency to "blow up" early on, due to its sensitivity to sudden increases in observed species richness as samples are accumulated (Figure 3.6). Silva and Coddington (1996) used the Michaelis–Menten model to estimate the species richness of spiders at Pakitza in Peru and found that although the fit to a species accumulation curve was good overall, the number of species was underestimated for large numbers of samples, as well as for small ones. This led them to express concern that (extrapolated) species richness estimates would be deflated.

Colwell and Coddington (1994) were concerned that the shape of the species abundance distribution, which will be influenced by the taxon and environment under study, might constrain the effectiveness of the Michaelis–Menten and other models. This prediction was confirmed by Keating and Quinn (1998) who showed that the performance of the Michaelis–Menten model did indeed vary with assemblage structure. In their study they simulated assemblages whose species abundance distributions followed either MacArthur's broken stick model or Tokeshi's (1990, 1993) random fraction model (see Chapter 2 for further details). Assemblages consisted of 10, 100, or 1,000 species. Estimates of $S_{\max}$ and

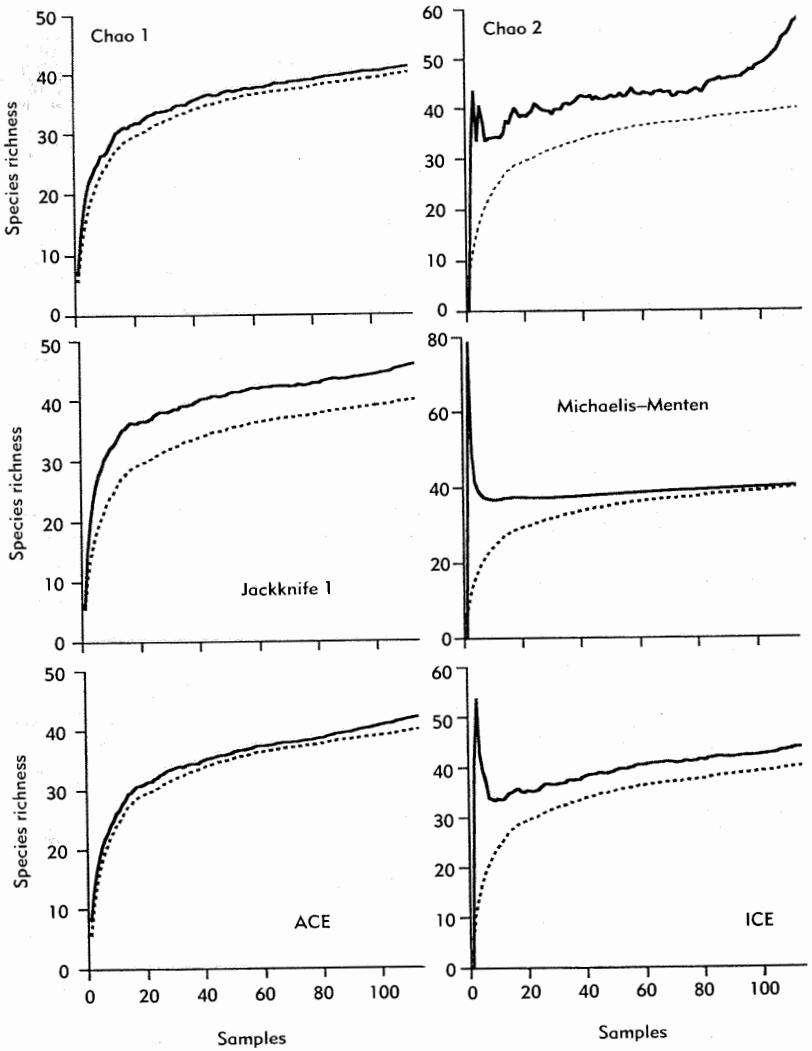

Figure 3.6 Performance of six richness estimators in relation to a known universe—the freshwater fish of Trinidad and Tobago. In each case the observed species accumulation curve (dotted line) is plotted alongside the estimated accumulation curve (solid line). Note that the *y* axis is scaled to accommodate the estimated curve; in all cases the observed curve is identical. There were 114 samples. Abundance data (number of individuals) were collected. See text and Phillip (1998) and Magurran and Phillip (2001a, 2001b) for further details. It is probable that the true species richness of the fauna is in the region of 40.

B for the two larger broken stick assemblages were unbiased but both parameters were overestimated in the small, 10-species assemblage. Even larger, and highly significant, deviations were observed with the random fraction model. S_{max} was underestimated by between 7% and 37% (all three assemblages, $P < 0.001$) and *B* by between 67% and 80% (assemblages of 100 and 1,000 species, $P < 0.001$). A similar level of underestimation was observed when the method was applied to a natural assemblage of vascular plants in Glacier National Park in Montana. Keating and Quinn (1998) argue that the Michaelis–Menten approach is thus of limited utility, especially since most assemblages would be better described by the random fraction than the broken stick model. None the less, Toti *et al.* (2000) concluded that it was the most useful estimator in a study of a spider assemblage in the Great Smoky Mountains while Chazdon *et al.* (1998) found that the model performed well in their investigation of woody regeneration in Costa Rica.

Irrespective of the method used, the estimates of the asymptote will be improved if the order in which samples are accumulated is randomized many times (Palmer 1991). Colwell and Coddington (1994) used 100 randomizations of sample order in their study and Chazdon *et al.* (1998) recommend that the minimum number of randomizations required needs to be assessed separately for each investigation.

Nonasymptotic curves can also be used to estimate species richness. These curves are familiar territory for every ecologist versed in the nature of species–area relationships. Gleason (1922) proposed that the relationship between species and area was best described by a log linear model, that is one in which the number of species increments increase arithmetically as the area increases logarithmically. MacArthur and Wilson (1967) advocated a log–log relationship, and recognized that area (*A*) was a surrogate for *N*, the total number of individuals across all species. (The assumption that this relationship between *S* and *A* is ultimately underpinned by a log normal distribution can be used to explain the range of "z" values typically observed in island biogeography (May 1975; Diamond & May 1981).) Palmer (1990) tested these models and found that the log–log relationship substantially overestimated true species richness. Although Palmer concluded that the log linear model was more effective, Colwell and Coddington (1994) argue that nonparametric methods (see below) are superior. Baltanás (1992), following Stout and Vandermeer (1975), imposed an asymptote on the log–log species–area curve to avoid the extremely high estimates of species richness generated when the curve is extrapolated to larger areas. However, although this method offered an improvement on the previous approach the results were not encouraging and the log–log model's performance was strongly affected by patchiness and overall species richness. Furthermore, it was less effective than two other methods applied to the

same data set: a parametric one based on the log normal distribution and the nonparametric first-order jackknife (Heltshe & Forrestor 1983). These methods are described in the next section.

Parametric methods

If the shape of a species abundance distribution can be satisfactorily described, it is theoretically possible to estimate overall species richness, or at the very least, the increase in S expected for an additional sampling of N. This approach is intuitively appealing. After all, once the parameters of a distribution have been established the rest ought to be straightforward. Unfortunately, problems in fitting distributions, and issues such as the veil line (Chapter 2), seriously hamper the endeavor.

The two species abundance models with the greatest potential in this context are the log series and log normal distributions (Colwell & Coddington 1994). Of these the log series distribution is the easiest to fit and the simplest to apply. However, since the log series distribution always predicts that the largest class will be the one represented by a single individual (Chapter 2), the estimate of species richness is nonasymptotic, that is, it will rise as the number of individuals sampled increases. None the less, Colwell and Coddington (1994) point out that it is possible to accurately predict the number of new species that will be encountered if the sample is increased. They also suggest that if the total number of individuals in a target area can be estimated, a good estimate of total species richness is possible. Hayek and Buzas (1997) describe the method and call the procedure "abundification." It begins by noting that a log series distribution of individuals amongst species assumes the following relationship between S (total number of species), N (total number of individuals), and α (the log series diversity index):

$$S = \alpha \ln(1 + N/\alpha)$$

(see p. 30).

We can use this equation to calculate the number of species that a community would be expected to have for any specified number of individuals. α is calculated using the observed number of species (S) and the observed number of individuals (N) and is then used to deduce the number of species that would be found for a larger N. To do this the new higher value of N is substituted in the equation. The method works best if the data conform to a log series distribution; S will be underestimated where they do not. This approach can also be used during rarefaction (Chapter 5). Rarefaction asks how many species would be found if sampling effort (usually number of individuals) is reduced to a specified level. This permits comparisons amongst communities where sampling effort has been unequal.

The log normal distribution opens a much larger can of ecological worms. Few natural distributions are perfectly symmetric, being instead truncated or log left-skewed (Chapter 2). If the mode of the distribution is evident it is at least possible to fit the distribution, but, as was apparent in Chapter 2, there is no consensus on how best to do this. Most people adopt the pragmatic approach of fitting a continuous log normal (see, for example, Worked example 2; Silva & Coddington 1996), although, strictly speaking, this is inappropriate since the observed data are in a discrete form (Pielou 1975; Colwell & Coddington 1994). Choosing the abundance classes is also problematic because the estimated parameters, and overall species richness, will vary depending upon whether $\log_2$, $\log_{10}$, or another log base is used. Knowing what to do with singletons is another challenge (Colwell & Coddington 1994). Following Pielou (1975), I (Magurran 1988) set the class boundaries at $x + 0.5$ because this insures that abundance data, which are integer values (at least in the case where abundance is measured as numbers of individuals), can be unambiguously assigned to classes. Ludwig and Reynolds (1988), by contrast, divide singletons between the first two classes, and doubletons between the second and third. As Coddington *et al.* (1991) note, this procedure has the effect of creating a mode in the second or third class and thus giving the appearance of a log normal distribution, even where one might not genuinely exist. Once again, the choice of class boundaries will influence the estimate of the mean and variance of the distribution as well as of total species richness. A final concern, and perhaps the most serious of all, is that there is still no method of generating a confidence interval on any estimate of species richness achieved via a continuous log normal distribution (Pielou 1975; Coddington *et al.* 1991; Colwell & Coddington 1994; Silva & Coddington 1996). The alternative, and more appropriate, Poisson log normal (Bulmer 1974) is harder to fit and thus rarely utilized. Colwell and Coddington (1994) noted that the Poisson log normal produced the highest estimates of species richness of any of the methods they tested.

Despite these caveats a number of investigators have used the log normal to estimate the species richness of an assemblage. Coddington *et al.* (1996), for example, wished to know the species richness of spiders in an Appalachian cove hardwood forest. A total of 89 species were observed across all samples. The Poisson log normal gave by far the highest estimate of richness at 182 species. Unfortunately, large confidence intervals (±126) rendered the estimate almost meaningless. The continuous log normal produced an estimate of 114 species, the second lowest after the Michaelis–Menten. Although this seems a plausible figure, the ab-

sence of a variance measure seriously limited its usefulness. Coddington *et al.* (1996) encountered problems when fitting the continuous (truncated) log normal distribution to their data. Other measures, such as the Chao and jackknife estimators (see below) performed more effectively and presented fewer computational challenges although it appeared that species richness was underestimated. And while the abundance distribution of Costa Rican ants surveyed by Longino *et al.* (2002) was clearly log normal, other estimates of richness estimation were more effective. One problem with nonparametric estimators such as the Chao and jackknife ones is that they are sensitive to sample size. If the assemblage is undersampled then its diversity will be underestimated. In theory, the log normal approach ought to avoid this problem, so long as it is possible to achieve a reasonably accurate estimate of the parameters. In practice, of course, it does not. Silva and Coddington (1996) observed that it is necessary to continue collecting common species in order to generate sufficient classes for a goodness of fit test. This is especially onerous and inefficient when tropical communities are under investigation. Slocomb and Dickson (1978) concluded that sample size needs to be large ($N > 1{,}000$) and to include ≥80% of species in the community before accurate estimates of species richness can be achieved by this approach.

Baltanás (1992) simulated log normally distributed communities that varied in richness, evenness, density, and aggregation. He then sampled these communities, estimated their richness, and concluded that his "Cohen" estimator (based on the parameters of the log normal distribution; see Chapter 2) performed better than the jackknife. It seems unlikely that this conclusion will hold for communities whose distribution deviates from the log normal distribution, or even for ones that fit it, but where the parameters cannot be accurately estimated.

Nonparametric estimators

There are, however, different—and more effective—means to the same end. Colwell and Coddington (1994) observe that the problem of estimating the number of unsampled cases is one that statisticians have been working on, in a variety of contexts, over many years. It is not only ecologists who need to predict the size of their universe; archeologists, epidemiologists, and even astronomers face parallel challenges (Bunge & Fitzpatrick 1993). In ecology, estimates of population size based on mark–recapture are subject to many of the same biases as their species richness counterparts. Colwell and Coddington (1994) and Chazdon *et al.* (1998) consider a number of nonparametric methods for the estimation of species richness, including some that have been adapted from mark–recapture analyses. These are termed nonparametric methods because they are not based on the parameter of a species abundance model that has previously been fitted to the data (see above), though, of course, as in virtually every other branch of diversity measurement, their performance depends on the underlying distribution. Many of the methods were devised by Anne Chao and her colleagues. They are both elegant and efficient and offer probably the most significant advance in diversity measurement in more than a decade. The measures are intuitively easy to understand and to use, even for a field ecologist with limited computational facilites. Their accessibility is further increased by Robert Colwell's (2001) EstimateS program.[2] This program was used to generate the examples that follow, and it is strongly recommended to anyone who wishes to estimate species richness in ecological assemblages.

The first method is Chao's (1984) simple estimator of the absolute number of species in an assemblage. It is based on the number of rare species in a sample. Colwell and Coddington (1994) call this measure Chao 1. The notation follows Chazdon *et al.* (1998):

$$S_{\text{Chao 1}} = S_{\text{obs}} + \frac{F_1^2}{2F_2}$$

where S_{obs} = the number of species in the sample; F_1 = the number of observed species represented by a single individual (singletons); and F_2 = the number of observed species represented by two individuals (doubletons). The variance of the estimate may also be calculated (Chao 1987; Colwell 2000).

The estimate of species richness produced by Chao 1 is a function of the ratio of singletons and doubletons and will exceed observed species richness by ever greater margins as the relative frequency of singletons increases. No further increase in the estimate is achieved once every species is represented by at least two individuals and at this point (one that is rarely reached during sampling) the inventory can be considered complete (Coddington *et al.* 1996). An obvious disadvantage of the Chao 1 method is that it requires abundance data (at least to the extent of knowing which species are singletons or doubletons) rather than presence/absence—often called incidence or occurrence—data. Colwell and Coddington (1994), however, note that, following the suggestion of Anne Chao, the same approach can be modified for use with presence/absence data by taking account of the distribution of species amongst samples. In this case it is necessary only to know the number of species found in just one sample and the number of species found in exactly two. They term this variant of the method Chao 2:

2 http://viceroy.eeb.uconn.edu/EstimateS. The EstimateS online user's guide provides more details on the methods.

$$S_{\text{Chao 2}} = S_{\text{obs}} + \frac{Q_1^2}{2Q_2}$$

where, Q_1 = the number of species that occur in one sample only (unique species); and Q_2 = the number of species that occur in two samples.

Colwell and Coddington (1994) also reviewed another category of estimators devised by Chao and Lee (1992), termed coverage estimators. This first generation of coverage estimators consistently overestimated species richness, especially at small sample sizes (Colwell & Coddington 1994). Chao and her collaborators have now developed new coverage estimators (Chao *et al.* 1993; Lee & Chao 1994) that appear to offer great potential (Chazdon *et al.* 1998). Coverage estimators are based on the recognition that species that are widespread or abundant are likely to be included in any sample and thus contain very little information about the overall size of the assemblage (Chao *et al.* 2000). In contrast it is the rare species that are most useful in deducing overall richness. The **a**bundance-based **c**overage **e**stimator, known as ACE, is based on the abundances of species with between one and 10 individuals. This cut-off was selected on the basis of empirical data (Chao *et al.* 1993). The estimate is completed by adding on the number of abundant species, that is those represented by >10 individuals. The partner **i**ncidence-based **c**overage **e**stimator, ICE, focuses on species found in ≤10 sampling units. A related technique can be used to estimate the true number of species that two communities have in common (Chapter 6).

Following Chazdon *et al.* (1998), the abundance-based coverage estimate (ACE) is:

$$S_{\text{ACE}} = S_{\text{abund}} + \frac{S_{\text{rare}}}{C_{\text{ACE}}} + \frac{F_1}{C_{\text{ACE}}}\gamma^2_{\text{ACE}}$$

where S_{rare} = the number of rare species (≤10 individuals); S_{abund} = the number of abundant species (>10 individuals); N_{rare} = the total number of individuals in rare species; F_i = the number of species with i individuals (F_1 = the number of singletons); $C_{\text{ACE}} = 1 - F_1/N_{\text{rare}}$; and

$$\gamma^2_{\text{ACE}} = \max\left\{\frac{S_{\text{rare}}}{C_{\text{ACE}}}\frac{\sum_{i=1}^{10} i(i-1)F_i}{(N_{\text{rare}})(N_{\text{rare}}-1)} - 1, 0\right\}$$

γ^2_{ACE} estimates the coefficient of variation of the F_i's.

The incidence-based coverage estimate (ICE) is:

$$S_{\text{ICE}} = S_{\text{freq}} + \frac{S_{\text{infr}}}{C_{\text{ICE}}} + \frac{Q_1}{C_{\text{ICE}}}\gamma^2_{\text{ICE}}$$

where S_{infr} = the number of infrequent species (found in ≤10 samples); S_{freq} = the number of common species (found in >10 samples); m_{infr} = the number of samples with at least one infrequent species; N_{infr} = the total number of occurrences of infrequent species; Q_j = the number of species that occur in j samples (Q_1 = the number of uniques); $C_{\text{ICE}} = 1 - Q_1/N_{\text{infr}}$; and

$$\gamma^2_{\text{ICE}} = \max\left\{\frac{S_{\text{infr}}}{C_{\text{ICE}}}\frac{m_{\text{infr}}}{(m_{\text{infr}}-1)}\frac{\sum_{i=1}^{10} i(i-1)F_i}{(N_{\text{infr}})^2} - 1, 0\right\}$$

It is essential to remember that Chao's estimators provide **minimum** estimates of richness and that they assume homogeneity amongst samples (Chao, in press). For this reason it is inappropriate to attempt to estimate richness across sites where there are large compositional differences, for example along ecological gradients or mosaics.

Other species richness estimators were also initially developed to fulfil different functions. Burnham and Overton (1978, 1979) used jackknife statistics to estimate population size during mark–recapture. These methods were subsequently applied, with some success, to species richness estimation. They are called Jackknife 1, a first-order jackknife estimator that employs the number of species that occur only in a single sample (Burnham & Overton 1978, 1979; Heltshe & Forrestor 1983), and Jackknife 2, a second-order estimator, which, like the Chao 2 equation, takes both the number of species found in one sample only (Q_1) and in precisely two samples (Q_2) into account (Smith & van Belle 1984). Both require incidence data. In the following equations m is the number of samples:

$$S_{\text{Jack 1}} = S_{\text{obs}} + Q_1\left(\frac{m-1}{m}\right)$$

$$S_{\text{Jack 2}} = S_{\text{obs}} + \left[\frac{Q_1(2m-3)}{m} - \frac{Q_2(m-2)^2}{m(m-1)}\right]$$

The variances of both estimators can be calculated. See Heltshe and Forrestor (1983) for details of the variance of Jackknife 1 and Burnham and Overton (1978) for Jackknife 2.

Finally, it is possible to apply the bootstrap estimator derived by Smith and van Belle (1984). It too requires only incidence data. Burnham and Overton (1978) explain how to estimate the variance.

$$S_{\text{boot}} = S_{\text{obs}} + \sum_{k=1}^{S_{\text{obs}}} (1 - p_k)^m$$

Figures 3.6 and 3.7 examine the performance of a range of nonparametric estimators and the Michaelis–Menten estimator in relation to two assemblages. The first assemblage is the freshwater fish of Trinidad and Tobago (Figure 3.6), which were the focus of an intensive survey (Phillip 1998; Magurran & Phillip 2001a, 2001b) where every drainage system was examined. A total of 114 samples were taken and both species richness and abundance (number of individuals) data were collected. It is likely that the true species richness of the fauna is close to 40 (Kenny 1995; Phillip & Ramnarine 2001). All of the measures tested, with the exception of Chao 2, produced results broadly consistent with this expectation. Interestingly, the Michaelis–Menten and ICE measures produced stable and broadly accurate estimates at small numbers of samples. However, it is also apparent that the Chao 1 and ACE estimators do not tell us anything that S_{obs} does not. A comparison of Chao 1 with Chao 2 and ACE with ICE reveals that the fish samples are heterogenous. This pattern arises because there are many more uniques than singletons and it is why Chao 1 and ACE fail (R. K. Colwell, personal communication; Chazdon *et al.* 1998).

What is the outcome when the size of the universe is unknown? Figure 3.7 uses occurrence data on beetle species in 125 5 × 5 km grid squares in Fife, Scotland. A total of 612 species have been recorded but this is likely to be a considerable underestimate. Only two of the measures tested—the Chao 2 and the ICE—produce estimates that are no longer incrementing when all the samples have been accumulated, although the Jackknife 2 and Michaelis–Menten graphs also show some signs of leveling off. What is intriguing is that these four approaches generate estimates that are not only markedly larger than the observed richness, but that are also broadly similar (Chao 2 = 1,137, Jackknife 2 = 1,239, Michaelis–Menten = 1,197, ICE = 1,295). How many beetle species are likely to occur in Fife? We know that the land area of Fife is 1,305 km^2. (This apparent discrepancy in size arises because Fife is bounded on three sides by the sea and many of the grid squares in the above analysis were coastal ones.) This means that Fife covers approximately 0.5% of the total land area of mainland Britain (224,424 km^2). Chinery (1973) gives the number of recorded beetle species in Britain as >4,000. If we assume that area and species form a log–log relationship in which the slope, z, is

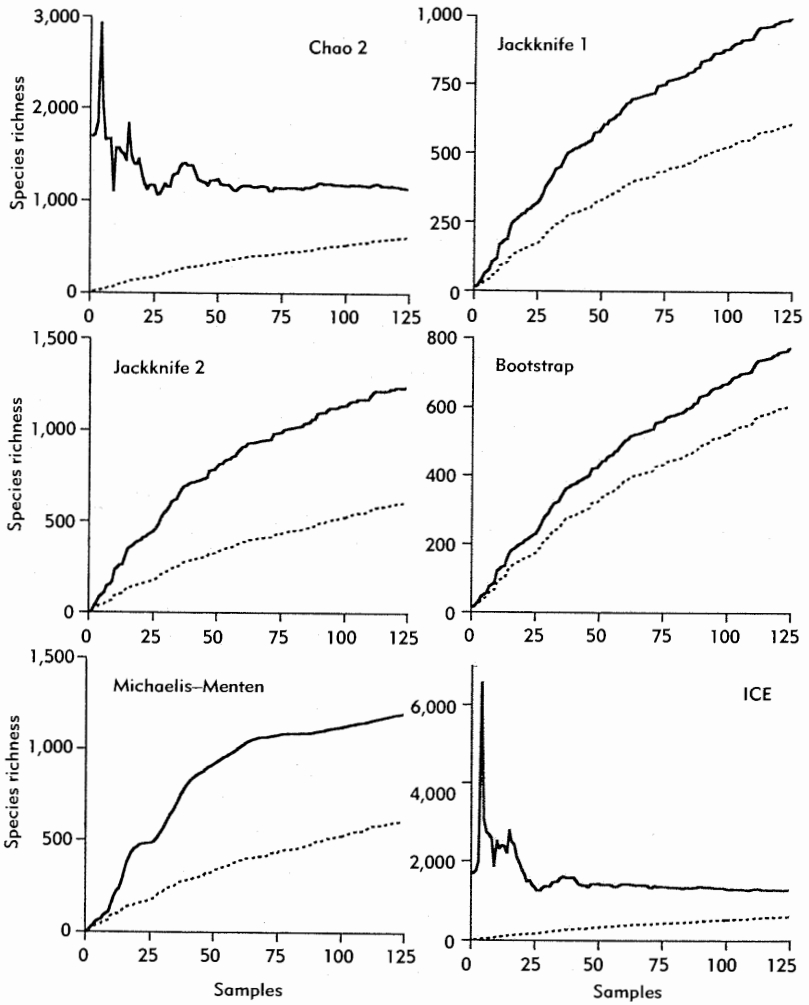

Figure 3.7 Performance of richness estimators in relation to an unknown universe — beetle species in Fife, Scotland. The observed species accumulation curve is shown as a dotted line and the estimated one as a solid line. There were 125, 5 × 5 km samples. Occurrence data are used. See text for further details. Note that the y axis is scaled to accommodate the estimated curve; in all cases the observed curve is identical. (Data courtesy of Fife Nature.)

0.25, the number of beetle species in Fife will be in the order 20% of the British total—in other words at least 800 species. (Reducing z to ≤0.21, in line with values more typically associated with mainland species–area curves (Diamond & May 1981; Rosenzweig 1995), will have the effect of

increasing this estimate.) The results provided by the estimators are plausible.

To date there have been relatively few comparative tests of these measures though it is already clear that they represent a powerful tool for ecologists. Colwell and Coddington (1994) tested the performance of these approaches (excluding ACE and ICE, which did not exist then). Their measure of success was the ability of the various estimators to predict the total species richness of a Costa Rican seed bank. Two of the estimators, Chao 2 and Jackknife 2, performed particularly well and produced remarkably accurate predictions of species richness from small numbers of samples. Walther and Martin (2001) used data from bird assemblages in Canada's Queen Charlotte Islands to test seven nonparametric and 12 accumulation curve methods. They concluded that the Chao estimators (followed by the jackknife estimators) were the least biased and most precise. Palmer (1990, 1991) (who could not examine the Chao estimators as they were not then available to him) found that the jackknife approach produced better estimates than bootstrapping. Poulin (1998) showed that both the Chao and jackknife methods were imprecise, relative to bootstrapping, if the assemblage contained many rare species. Condit *et al.* (1996) also observed that both the Chao and jackknife estimators substantially underestimated the true species richness of woody plants in fully censused 50 ha plots in three tropical forests. However, since Condit *et al.*'s study used local samples to deduce the richness of a heterogenous universe an underestimate was probably inevitable. In their neotropical spider study, Silva and Coddington (1996) observed that Chao 1 and Chao 2 provided higher, and likely more realistic, estimates in cases of undersampling, than the jackknife method, but concluded that since the jackknife was a conservative estimator agreement between it and other estimators might signify a robust result. A similar ranking of measures occurred in an investigation of a temperate spider community in which Coddington *et al.* (1996) found the Chao 1 and Chao 2 estimates exceeded the jackknifed one.

Chazdon *et al.* (1998) recognized that estimators must be evaluated using a range of criteria. They identified sample size, patchiness, and overall abundance (i.e., total number of individuals in the sample) as being important and assessed the performance of the nonparametric estimators (as well as the Michaelis–Menten model) using data collected during a census of woody regeneration (seedlings and saplings) in primary and secondary forest in Costa Rica. The Michaelis–Menten estimator emerged as being most stable across all sample sizes, whereas Chao 2, ICE, and Jackknife 2 increased steadily with sample size. Patchiness[3] had

3 Colwell's EstimateS program contains an option for simulating patchiness.

an important influence on the outcome. Chazdon *et al.* (1998) found that the rate at which new species were encountered with increasing sample size was reduced as the distribution of species changed from being random to being progressively more patchy. The Chao 1 and ACE measures were especially sensitive to patchiness, and were effective only in cases where species were randomly distributed. On the other hand, the Chao 2 and ICE estimators performed well at moderate levels of patchiness, though not at high ones. This contrast is rooted in the differences between the abundance and incidence measures. When species are distributed randomly the number of singletons and uniques are identical, as are the number of doubletons and duplicates for the same set of samples. However, as patchiness increases, progressively more species are detected in one sample only. The Michaelis–Menten measure increased with degree of patchiness and the jackknife and bootstrap estimators became more dependent on sample size as patchiness intensified. Total abundance of individuals also had an effect. In the three primary forests in the study, abundance (N) was highly correlated with species richness and Chazdon *et al.* (1998) were concerned that this relationship might obscure genuine richness differences between sites. Although none of the estimators completely satisfied all criteria in terms of their particular data set they concluded that the ICE was most promising while the Chao 2 estimator also performed well at small sample sizes. The Jackknife 2 and Michaelis–Menten were also viewed as useful estimators and together these four were identified as worthy of further exploration.

Most tests of estimator performance involve either small, well-inventoried assemblages or large, but incompletely, studied areas of unknown richness. An important contribution has been provided by Longino *et al.* (2002) who conducted an intensive investigation of ant species in Costa Rica's La Selva Biological Station. This 1,500 ha site is exceptionally well studied and is known to contain at least 437 resident ant species. Eight different categories of sampling method were employed, and nearly 2,000 samples collected. These samples contained just under 8,000 species occurrences. Three richness estimators—the area under the log normal curve, the Michaelis–Menten method, and ICE—were evaluated in the context of a smoothed species accumulation curve. None of the methods produced a stable asymptote though they all tended to converge on observed species richness at large sample size. However, the Michaelis–Menten and ICE estimators outperformed the log normal-derived estimates on almost all occasions. Longino *et al.* (2002) conclude that rarity is one factor that causes estimators to fail. Importantly, the authors point out that levels of rarity are exaggerated (in surveys of insect assemblages) when a single sampling technique is employed. This issue is revisited in Chapter 5. Moreover, Longino and his colleagues stress the need for the continued evaluation of estimators.

Sampling considerations and stopping rules

As the preceding examples have illustrated, the performance of nonparametric estimators is often assessed in relation to an empirical species accumulation curve. Unless the assemblage has been sampled exhaustively, this curve will underestimate species richness to an unknown degree. Collectors vary in their efficiencies (Coddington *et al.* 1991) and sampling is usually more challenging in some habitats and weather conditions than in others. Organisms, especially mobile ones, can be arduous to sample at certain times of day, or may show seasonal variation in abundance.

This uncertainty leads to a classic "catch 22" situation. An investigator needs to be relatively confident that the sample is big enough to provide an accurate estimate of the size of the assemblage without knowing in advance how large the assemblage actually is. This means that empirical "stopping rules" are invaluable. A "stopping rule," as the name implies, is an indication of the point beyond which further sampling is no longer necessary or at which it is too costly.

The asymptotic nature of the Michaelis–Menten estimator means that it has potential application as a stopping rule. One rule of thumb is to continue sampling until the empirical species accumulation curve crosses the one generated by the Michaelis–Menten model and then to use a nonparametric method (discussed above) to estimate total richness (P. A. Henderson & A. E. Magurran, unpublished study).[4] Another suggestion is provided by Colwell and Coddington (1994). They note that a census can be treated as complete if all species have an abundance of two or greater (if relative abundance data are being collected) or if they all occur in at least two samples (when occurrence data are used). This method is sound but may be unduly onerous when there are many singletons (Chapter 2).

A useful check is to subdivide the total sample into two parts (at random) and estimate the richness of these separately. If they give answers that are consistent with the one obtained for the combined sample the investigator can be confident that ample data have already been collected. Krebs (1999) provides general advice on the use of stopping rules in ecology and the next two chapters address the issue of sample size in diversity measurement in more detail.

Estimators that are unstable or still rising when all samples have been included do not provide a reliable estimate of species richness. However, Longino *et al.* (2002) note that in such circumstances Chao estimators can be used to derive a valid minimum estimate of richness.

4 This method is included in Species Diversity and Richness (http://www.irchouse.demon.co.uk/).

Overview of estimators

What then, in summary, do we, as ecologists, require from such richness estimators? Since time and money are almost always in short supply we need to accurately predict the total species richness of an assemblage, using as small a sample size as possible. Indeed a key attribute of estimators is independence from sample size above some minimum size of sample (Longino *et al.* 2002). Ideally, we should be able to independently check the accuracy of the estimate. Stopping rules need to be tested and refined. The measure should be robust against slight variations in sampling protocol. An estimate of variance should be possible, and the confidence limits should not be so wide as to render the estimate meaningless. The estimators should not be biased by variation in the underlying species abundance distribution. They should also be computationally efficient, though this requirement becomes ever less important as computers improve and packages such as EstimateS become available.

In view of their performance and relative simplicity, richness estimators hold great promise for the future. By adopting both species accumulation curves and jackknife or Chao methods it is possible to obtain not only a meaningful "picture" of the species diversity of the assemblage, but also a good estimate of its total richness. A related question, estimating the number of shared species in two assemblages (Chao *et al.* 2000), is explored in Chapter 6.

Other considerations

Lande *et al.* (2000) have reported a potential weakness in species accumulation curves. They note that estimates of species are unreliable when species richness curves intersect, as they will do if one assemblage has more species overall but lower Simpson diversity (equivalent to reduced evenness) (Figure 3.8). Such an effect could arise as a consequence of disturbance, which, at an intermediate level, may increase both the richness of an assemblage, and the variance of the species abundance distribution (i.e., lower evenness) (Connell 1978). (High levels of disturbance tend to further amplify the variance in species abundances but may ultimately reduce richness.) Investigations that set out to contrast disturbed sites with their pristine equivalents may thus be especially prone to this shortcoming.

Lande *et al.* (2000) illustrate the problem with reference to two neotropical rain forest butterfly communities, one of which they classify as "intact," and the other as "disturbed." At small or even moderate sample sizes the observed species abundance curves are less effective than a random guess at ranking the assemblages accurately. It is only at

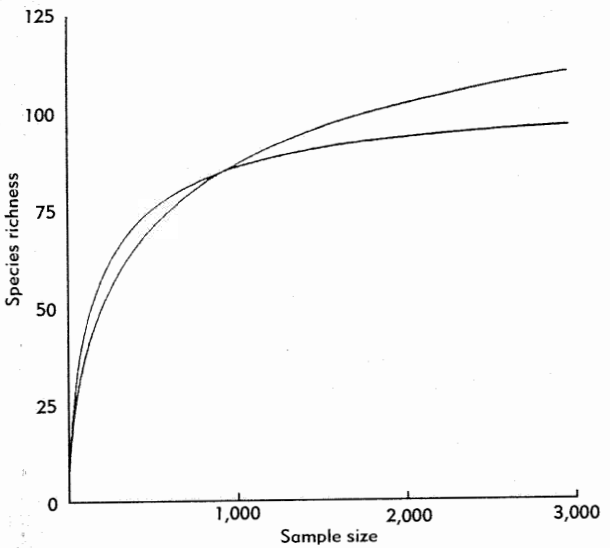

Figure 3.8 Expected species accumulation curves in two lowland Amazonian butterfly assemblages. The curve with the initial lower slope and higher asymptote represents a disturbed assemblage, the other curve an intact one. Expected accumulation curves were derived from fitted log normal distributions of species abundance. (Redrawn with permission from Lande *et al.* 2000; further details are provided in their paper.)

points above the intersection of the curves that the probability of ranking the communities in the correct manner exceeds 50%. By contrast, the Simpson index correctly ranks communities at a sample size over 20 times smaller (81 individuals as opposed to 1,801 individuals). Of course the Simpson index has the drawback of requiring abundance data, but this disadvantage could well be traded off against the requirement of a smaller sample size. It is also worth noting that Lande *et al.* (2000) fitted a log normal to empirical data and then used the parameters of that (perfect) log normal to demonstrate that the unbiased estimator of the Simpson index is independent of sample size (because the estimator does not include N). The Simpson index calculated directly from empirical data sets, including those that are not log normal, may produce less satisfying results. Furthermore, as May (1975) points out, Simpson's index will increase with S, once $S > 10$, if the data follow a log normal distribution (but not if they are described by the log series). The underlying species abundance distribution thus affects even this method.

As Lande *et al.* (2000) recognize, the difficulty with species accumulation curves, and extrapolations based thereon, is that in order to judge the validity of the estimates they generate one needs either an independent evaluation of overall species richness or a knowledge of the underlying species abundance distribution. The user must be sensitive to their shortcomings and alert to the possibility of intersecting accumulation curves. Lande *et al.* (2000) offer the wise advice that ecologists and conservationists should employ a measure of Simpson diversity as well as species richness when comparing communities. At the very least, and in the absence of abundance data, users of species richness measures ought to be vigilant for marked discontinuities in evenness amongst assemblages.

The problems encountered when comparing the diversity of communities, along with some solutions, are discussed further in Chapter 5.

Surrogates of species

It is not always possible to sample intensively enough to produce even a rough estimate of species number. Ecologists have therefore searched for other means of identifying areas with high species richness and of ranking sites along a rich–poor axis, often for conservation purposes. There are three main types of surrogacy: **cross-taxon**, where high species richness in one taxon is used to infer high richness in others (Mortiz *et al.* 2001); **within-taxon**, where generic or familial richness is treated as a surrogate of species richness (Balmford *et al.* 1996); and **environmental**, where parameters such as temperature or topograpical diversity are assumed to track species richness. Gaston (1996b) provides an overview. Surrogacy approaches are becoming increasingly popular and can in some instances successfully map richness gradients. For example, macrolichens emerged as a good indicator of the species richness of mosses, liverworts, woody plants, and ants in the Indian Garwhal Himalaya (Negi & Gadgil 2002), while certain higher-taxon clusters, for instance families of British butterflies and Australian birds (Williams & Gaston 1994) proved efficient predictors of species richness. Lee (1997) reports that family- and genus-level diversities are very good indicators of underlying species diversities. The increasing use of remote sensing holds open the promise of rapid biodiversity assessment (Gould 2000), but the complex nature of the relationship between environmental variation and biological diversity means that interpretation can be difficult. One simple and widely used application is to deduce species number from the area of particular habitat types, mostly famously Amazonian rain forest (see, for example, Brown & Albrecht 2001) although edge effects and other variables must be taken into account (Laurance *et al.* 2002).

There are some obvious disadvantages to surrogacy methods. Each taxon and system must be dealt with on a case by case basis. The fact that macrolichen diversity predicts ant diversity in the Indian Himalaya is no guarantee that it will be a good predictor elsewhere and the distribution of species amongst higher taxa can change from place to place (Gaston 1996b). Moreover, since these approaches do not measure species richness but simply identify sites where it may be high, the outputs are not directly comparable with those obtained using conventional estimates and measures. By the same token, sites where species richness has been measured using surrogate or direct methods cannot be ranked on the same axis.

How many species are there on earth?

The intellectual goal of deducing how many species there are on earth has received recent impetus in the light of the growing concerns about global species loss. In the paper that gave its name to the title of this chapter, May (1990) set out a variety of approaches for estimating the species richness of the planet. Many of these focus on insects, the taxon that contributes disproportionately to life on earth. These methods, which fall outside the scope of this book, are described in May (1988, 1990a, 1992, 1994b, 1999), Grassle and Maciolek (1992), Poore and Wilson (1993), and Hammond (1994). In summary, a variety of approaches, including projecting the rate at which new species are recorded (May 1990a), elucidating the relationship between body size and taxon richness, particularly for small organisms (Finlay 2002), and scaling up from the number of insect species per tree to reach a global total (Novotny *et al.* 2002), typically produce figures in the 5–10 million species range. This contrasts with the <2 million species that have been formally recorded. However, the confidence limits around the projected species totals remain high and a much deeper understanding of key habitats and species groups, such as tropical insect faunas and deep-sea macrobenthos, is urgently needed. Since the extent of global diversity is often inferred from the richness levels at local scales, methods for estimating species richness through extrapolation (described in this chapter) can help answer the question: "How many species are there on earth?" (May 1988). This point is revisited in the concluding chapter.

Summary

1 Species richness is often treated as the iconic measure of biological diversity, though it is by no means the only measure of biological diversity.

Its appealing simplicity masks a number of problems. Of these, the dependence of richness estimates on sampling intensity is the most onerous.

2 A number of nonparametric estimators, notably those developed by Anne Chao and her colleagues and popularized by Robert Colwell and his colleagues, provide a promising method of deducing total species richness using tractable sample sizes. They represent one of the most important advances in diversity measurement in recent years.

3 These approaches are evaluated in relation to methods based on the extrapolation of species accumulation curves and species abundance distributions.

4 While more tests are needed, especially in species-rich assemblages, richness estimators are an effective means of producing a valid minimum estimate of richness.

5 When species accumulation curves intersect ranking of assemblages is problematic. In such circumstances Lande and his colleagues recommend the use of the Simpson index since this consistently ranks assemblages (though it also necessitates the collection of abundance data).

chapter four

An index of diversity . . .[1]

Chapter 2 revealed how species abundance distributions can be used to describe the structure of communities and shed light on the ecological processes that underlie that structure. Chapter 3 reviewed methods of estimating species richness. Despite the recent progress on both these fronts there is still a perceived need for "indices" of diversity that capture both the richness and evenness characteristics of an assemblage. As there are endless ways of emphasizing different aspects of the species abundance relationship, the number of candidate diversity indices is infinite (Molinari 1996). However, because all measures must emphasize one or other component of diversity (richness or evenness), no perfectly unified diversity index is possible.[2] None the less, as the literature testifies, the challenge of devising ever better measures has been taken up by many ecologists over the years. As a result, there are a plethora of indices from which to choose and this diversity of diversity measures can make it difficult to select the best approach. The matter is complicated by the fact that the most popular indices are not necessarily the best.

My aim in this chapter is to provide a user's guide to diversity measures. It is not intended to be an exhaustive list. Instead, I review methods that are in common use as well as ones, that are, in my opinion, particularly effective. I describe potential applications, compare the performance of key measures with other competing methods, and highlight

1 After McIntosh (1967).

2 Clarke and Warwick (2001a) note that if many different diversity measures are calculated for a single set of samples and the outcome is ordinated using principal components analysis, the first two axes – which represent richness and evenness – will account for most of the variation.

Box 4.1 **How to choose a diversity index**

1 It is very tempting to calculate a range of diversity measures, especially if one is using a package that will do this automatically. This temptation must be resisted! It is important to know in advance which aspect of biodiversity is being investigated – and why – since this will have implications for the sampling design, etc., and not simply to choose the measure that provides the most attractive answer.

2 Sample size must be adequate to meet the objectives of the investigation. Advice on how to achieve this is given in the next chapter.

3 Replication is strongly recommended. All other things being equal it is almost always better to have many small samples rather than a single large one. Replication means that statistical analysis is possible and allows confidence limits to be constructed. Repeated sampling is also the key to species richness estimation (Chapter 3) and means that jackknifing and bootstrapping (Chapter 5) are feasible.

4 Consider whether a "heterogeneity" measure is really necessary. Since biological diversity is so often equated with species richness, a demonstrably robust estimate of the number of species may be the most useful outcome (Chapter 3).

5 If a heterogeneity measure is justified, consider using either α or Simpson's index. The performance of both is well understood and they are intuitively meaningful. α is relatively unaffected by sample size once $N > 1{,}000$. There is no need to confirm that species abundances follow a log series distribution. Simpson's index provides a good estimate of diversity at relatively small sample sizes and will rank assemblages consistently, even when species accumulation curves intersect. Confidence limits can be attached to both measures (Chapter 5).

6 Despite its popularity, use of the Shannon index needs much stronger justification. Given its sensitivity to sample size there appear to be few reasons for choosing it over species richness. Interpretation can also be difficult. Opting for exp H' (or Hill's N_1 measure; Chapter 5) does not overcome the fundamental problems associated with this measure. However, the Shannon index seems likely to persist, since many long-term investigations have chosen it as their benchmark measure of biological diversity.

7 The Berger–Parker index provides a simple and easily interpretable measure of dominance.

8 Likewise, there are advantages in using the Simpson evenness measure, particularly if the Simpson index has been used to describe diversity. Smith and Wilson (1996) provide sound advice if other evenness measures are sought (see also above).

9 Taxonomic distinctness measures are informative and easily interpretable and have the added advantage of being robust against variation in sampling effort.

potential advantages or limitations. Worked examples are provided to assist the user. Box 4.1 gives advice on how to select an appropriate measure.

Since even the most elegant methodology cannot redeem an ill-conceived investigation, the single most important consideration in the measurement of diversity is that the user has a clear idea of the objectives of the study. Is it intended to estimate the species richness of potential nature reserves? Is a measure of pollution stress required? Does the user need to assess the effects of disturbance? Are confidence

limits on the diversity estimate essential? Once the objectives have been clearly delineated it is relatively straightforward to select a diversity measure. Sampling must also be adequate for the purposes of the study (Chapter 5).

Diversity measures

As noted in Chapter 1, diversity statistics are conventionally classified as either **species richness** measures (McIntosh 1967) or **heterogeneity** measures (Good 1953). Heterogeneity measures are those that combine the richness and evenness components of diversity.[3] Evenness measures were later developed (by Lloyd and Ghelardi (1964) and subsequent workers) in an attempt to distil the evenness component of diversity into a single number. Evenness measures assess the departure of the observed pattern from the expected pattern in a hypothetical assemblage. This assemblage may either be completely uniform (all species equally abundant) or represent some biologically achievable pattern of evenness (such as the broken stick distribution; see Lloyd and Ghelardi (1964)).

Species richness measures and estimators were dealt with in Chapter 3. Heterogeneity (and evenness) measures, the focus of this chapter, fall into two categories—either a parameter of a species abundance model, for example log series α, or a measure, such as Simpson's diversity index D (Simpson 1949), that makes no assumption about the underlying species abundance distribution. For this reason such measures are sometimes described as nonparametric diversity indices. This does not mean, however, that they are necessarily robust against shifts in the pattern of species abundances.

"Parametric" measures of diversity

Log series α

The diversity index α is a parameter of the log series model. Its calculation is a necessary prelude to fitting the distribution (Chapter 2). However, when S (the number of species) and N (the total number of individuals) are known, α may be read directly from Williams's (1964) nomograph (duplicated in Southwood and Henderson (2000)) or from the table in Hayek and Buzas (1997, appendix 4). A series of studies (Kempton & Taylor 1974, 1976; Taylor 1978) investigating the properties of α have come out strongly in favor of its use, even when the log series distribution is not the best descriptor of the underlying species abundance pattern. Hayek and Buzas (1997) concur with this, as long as $x \geq 0.5$ (in other words if the ratio $N/S > 1.44$) and as long as $S > \alpha$. In fact x is almost always >0.9 (and often close to 1; see Figure 2.10 and the first equation on p. 30) and $S > \alpha$ in natural assemblages. Recall that the first term of the log series, which predicts the number of species, is αx. Thus, α is approximately equal to the number of species represented by a single individual. Moreover, as Chapter 2 showed, it is possible to attach confidence limits to α. α is relatively unaffected by variation in sample size, and completely independent of it if $N > 1{,}000$ (Taylor 1978).

3 Following Hurlbert (1971), many ecologists adopted the practice of restricting the term "diversity" to heterogeneity measures, that is those that combine richness and evenness. This convention appears to have weakened in the last decade, as popular interest in biological diversity, which is often treated as synonymous with species richness, has heightened.

Log normal λ

It might be expected that the standard deviation (σ) of a log normal distribution would be a good measure of diversity. Although σ can be used as an evenness measure it is a poor index for discriminating amongst samples and cannot be estimated accurately when sample size is small (Kempton & Taylor 1974). Nor is S^* a good predictor of total species richness (Chapters 2 and 3). Unexpectedly, however, the ratio of these parameters (S^*/σ) turns out to be an effective diversity measure (λ). λ discriminates assemblages well (Taylor 1978). Its ranking of sites (from high to low diversity) tends to accord well with α (Figure 4.1).

The *Q* statistic

The Q statistic, proposed by Kempton and Taylor (1976, 1978) is an interesting and innovative approach to diversity measurement. This measure is based on the distribution of species abundances but does not require the user to fit a model to the empirical data. Instead, a cumulative species abundance curve (of the empirical data) is constructed and the interquartile slope of this curve is used to measure diversity (Figure 4.2). In theory, as in an earlier index suggested by Whittaker (1972), the whole curve could be used to describe diversity, but the practice of restricting the measure to the interquartile region means that neither very abundant, nor very rare, species bias the outcome.

The following equation is estimated from empirical data:

$$Q = \frac{\frac{1}{2}n_{R1} + \sum_{R_1+1}^{R_2-1} n_r + \frac{1}{2}n_{R2}}{\ln(R_2/R_1)}$$

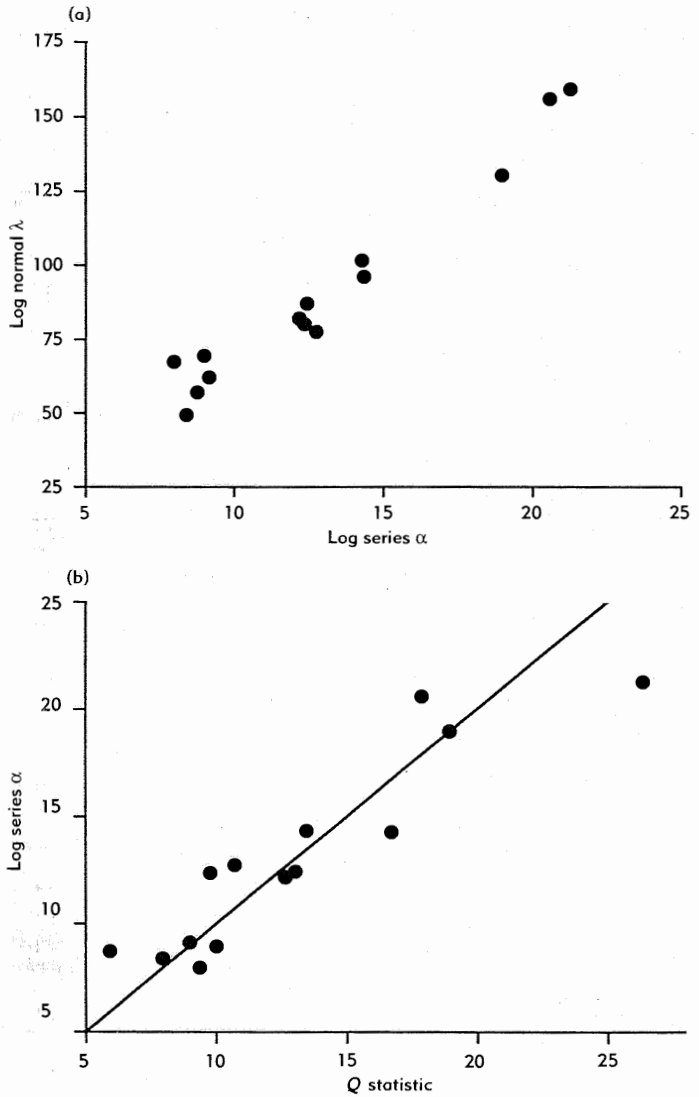

Figure 4.1 (a) Values of the log series index α and the log normal index λ tend to be strongly correlated. In this example depicting moth trap samples from an Irish woodland, $r = 0.98$. (b) Relationship between the Q statistic and the log series index α for the same data set ($r = 0.92$). The line $Q = \alpha$ is also shown.

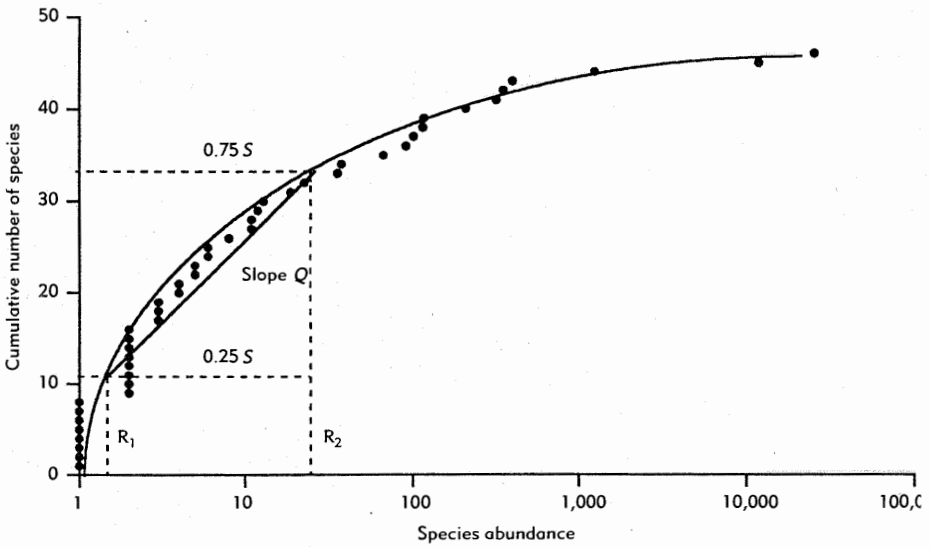

Figure 4.2 Illustration of the Q statistic. The x axis shows species abundance of a fish assemblage caught in Sulaibikhat Bay, Kuwait on a logarithmic ($\log_{10}$) scale while the cumulative number of species is displayed on the y axis. R_1, the lower quartile, is the species abundance at the point at which the cumulative number of species reaches 25% of the total. Likewise R_2, the upper quartile, marks the point at which 75% of the cumulative number of species is found. The Q statistic measures the slope Q between these quartile. (Data from table 1, Wright 1988.)

where n_r = the total number of species with abundance R; R_1 and R_2 = the 25% and 75% quartiles; n_{R1} = the number of species in the class where R_1 falls; and n_{R2} = the number of species in the class where R_2 falls.

The quartiles are chosen so that:

$$\sum_{1}^{R_1-1} n_r < \frac{1}{4}S \leq \sum_{1}^{R_1} \quad \text{and} \quad \sum_{1}^{R_2-1} n_r < \frac{3}{4}S \leq \sum_{1}^{R_2}$$

where S = the total number of species in the sample; although the placement of R_1 and R_2 is not critical as the interquartile region of a cumulative species abundance curve, or indeed a rank/abundance plot, tends to be linear. In the case of a rank/abundance plot the slope $1/Q$ is used (see Worked example 6).

Kempton and Wedderburn (1978) point out that Q, expressed in terms of the log series model, is analogous to α. For the log normal model $Q = 0.371\ S^*/\sigma$ ($= 0.371\lambda$). The congruence between these three diversity measures is clearly illustrated in Figure 4.1. Thus, while Q is not formally a parametric index its performance is similar to those that are.

Although Q may be biased in small samples, this bias is low if >50% of the species in the community have been censused (Kempton & Taylor 1978). Despite its simplicity and ease of interpretation the Q statistic has not been widely adopted by ecologists. Pettersson (1996), however, used it when comparing the diversity of spiders in lichen-rich, natural spruce *Picea abies* forests in northern Sweden with selectively logged, lichen-poor forests. Spider diversity was found to be higher in the unlogged forests. (Interestingly, rarefaction plots—see Chapter 5—also used by Pettersson (1996) indicated no differences between the sites apart from a lower abundance of spiders on branches in lichen-poor forests.) Ghazoul (2002) also adopted the measure to track shifts in butterfly diversity in relation to disturbance level in a tropical dry forest in Thailand. An evenness measure, conceptually similar to the Q statistic, has been proposed by Nee *et al.* (1992) (see below).

"Nonparametric" measures of diversity

Most diversity measures are not explicitly associated with named species abundance models even though their performance is often governed by the underlying distribution of species abundances. The next section investigates a number of these so-called "nonparametric" measures of diversity and assesses their utility.

Information statistics

One of the most enduring of all diversity measures is the Shannon index. Such endurance is all the more remarkable in light of the fact that most commentators who discuss the relative merits of the various methods of measuring diversity go out of their way to underline the disadvantages of the Shannon index (May 1975; Magurran 1988; Lande 1996; Southwood & Henderson 2000). Inertia, however, has insured that this measure will not go quietly. Many people feel happier about adopting a measure with a long tradition of use, even if it has not stood the test of time. Its origins in information theory and its association with concepts such as entropy likely also contribute to its continuing appeal (Martín & Rey 2000).

Shannon and Wiener independently derived the function that is now generally known as the Shannon index or Shannon information index, though sometimes mistakenly referred to as the Shannon–Weaver index (Krebs 1999)—a misunderstanding that arose because the original formula was published in a book by Shannon and Weaver (1949). The index is based on the rationale that the diversity, or information, in a natural system can be measured in a similar way to the information contained in a code or a message. It assumes that individuals are randomly sampled

from an infinitely large community (Pielou 1975), and that all species are represented in the sample. The Shannon index is calculated from the equation:

$$H' = -\sum p_i \ln p_i$$

The quantity p_i is the proportion of individuals found in the ith species. Worked example 7 illustrates the calculations. In a sample the true value of p_i is unknown but is estimated using its maximum likelihood estimator, n_i/N (Pielou 1969). Since the use of n_i/N to estimate p_i produces a biased result, the index should, strictly speaking, be obtained from the following series (Hutcheson 1970; Bowman *et al.* 1971):

$$H' = -\sum p_i \ln p_i - \frac{S-1}{2N} + \frac{1-\sum p_i^{-1}}{12N^2} + \frac{\sum\left(p_i^{-1}-p_i^{-2}\right)}{12N^3} + \ldots$$

In practice, however, this error is rarely significant (Peet 1974) and all the terms in the series after the second are very small indeed. A more substantial source of error arises when the sample does not include all the species in the community (Peet 1974). This error increases as the proportion of species represented in the sample declines. As the true species richness of an assemblage is usually unknown for all the reasons discussed in Chapter 3, an unbiased estimator of the Shannon index does not exist (Lande 1996).

For historical reasons $\log_2$ is often used when calculating the Shannon diversity index. There are no pressing biological reasons why this tradition should be preserved. Indeed it is computationally simpler, and ecologically just as valid, to use natural logs ($\log_e$, also known as ln) or even $\log_{10}$ in the equation. There is an increasing trend towards standardizing on natural logs (see, for example, Cronin & Raymo 1997) and it is essential to use these in the series (shown above). What is important is to be consistent in the choice of base when comparing diversity between samples or studies or when using the Shannon index to estimate evenness (see the equation on p. 108).

Pielou (1969) lists the terms used to describe the units in which the Shannon index measures diversity. These stem from information theory and depend on the type of logarithms used. "Binary digits" or "bits" apply when $\log_2$ is adopted, "natural bels" or "nats" when it is $\log_e$, and "decimal digits" or "decits" for $\log_{10}$. These terms are rarely applied these days, a sensible trend since they do not assist in the interpretation of estimates of diversity. However, references to bits and nats do crop up from time to time in the older literature.

The value of the Shannon index obtained from empirical data usually falls between 1.5 and 3.5 and rarely surpasses 4 (Margalef 1972). It is only

when there are huge numbers of species in the sample that high values are produced. May (1975) notes that, given a log normal pattern of species abundance, 10^5 species would be needed to produce a value of $H' > 5.0$.

The fact that the Shannon index is so narrowly constrained in most circumstances can make interpretation difficult. The ecologist confronted by values of $H' = 2.35$ and $H' = 2.47$ may have little idea whether the two sites in question have similar diversities or are substantially different. (A similar criticism can be directed towards the log series index α.) Some investigators sidestep the problem by using $e^{H'}$ instead of H'. $e^{H'}$ is an intuitively meaningful measure as it gives the number of species that would have been found in the sample had all species been equally common (Whittaker 1972). Thus, $H' = 2.35$ becomes $e^{H'} = 10.49$ and $H' = 2.47$ becomes $e^{H'} = 11.82$. Kaiser *et al.* (2000) used this approach when examining the effects of chronic fishing disturbance on marine benthic communities. Transforming the index has the useful function of spreading the values out, but it still does not shed much light on whether estimates of diversity are significantly different or not. $e^{H'}$ is equivalent to Hill's N_1 diversity index (Chapter 5).

A better approach, assuming that there is an a priori hypothesis why one assemblage should be more or less diverse than another, is to employ a statistical test. In the past one of the only options was to use Hutcheson's (1970) "*t*" test for the Shannon index. Hutcheson (1970) sets out the method for calculating the variances of the two estimates, the value of *t* and the degrees of freedom used to assess significance. However, Taylor (1978) pointed out that when the Shannon index is calculated for a number of sites, the indices themselves will be normally distributed. This property makes it possible to use parametric statistics, including powerful analysis of variance methods (Sokal & Rohlf 1995), to compare sites for which diversity has been calculated (see, for example, Kaiser *et al.* 2000). Recently, attention has switched to resampling procedures such as bootstrap and jackknife methods (Lande 1996). This approach, which has much to recommend it, is discussed in Chapter 5.

The Shannon evenness measure

As a heterogeneity measure the Shannon index takes into account the degree of evenness in species abundances. None the less, it is possible to calculate a separate evenness measure. The maximum diversity (H_{max}) that could possibly occur would be found in a situation where all species had equal abundances, in other words if $H' = H_{max} = \ln S$. The ratio of observed diversity to maximum diversity can therefore be used to measure evenness (J') (Pielou 1969, 1975):

$$J' = H'/H_{max} = H'/\ln S$$

Beisel and Moreteau (1997) provide a simple method of calculating H_{min}, a value used in other forms of the Shannon evenness (see Hurlbert 1971).

Heip's index of evenness

Heip (1974) felt that evenness measures should not be dependent on species richness (which Pielou's J' is, up to approximately $S = 25$ (Smith & Wilson 1996)) and that they should have a low value in contexts where evenness is obviously low. His proposed measured was intended to meet these criteria:

$$E_{Heip} = \frac{(e^{H'} - 1)}{(S - 1)}$$

Although E_{Heip} is less sensitive to species richness than J', it does not meet the requirement of being independent of sample size when there are fewer than about 10 species in the sample (Smith & Wilson 1996). It does, on the other hand, satisfy the expectation of attaining a low value when evenness is low (see Table 4.1, p. 120). Smith and Wilson (1996) showed that the minimum value of Heip's measure is 0 and that it registers 0.006 when an extremely uneven community (with species abundances 1, 497, 1, 1, 1) is used.

SHE analysis

One of the problems with the Shannon index is that it confounds two aspects of diversity: species richness and evenness. This is often viewed as a disadvantage since it can make interpretation difficult; an increase in the index may arise either as a result of greater richness, or greater evenness, or indeed both. However, Buzas and Hayek (1996) and Hayek and Buzas (1997) realized that this characteristic of the Shannon index can actually be turned to an advantage. Their reasoning is as follows. They first note that one measure of evenness is $E = e^H/S$ (Heip 1974; see also discussion above) and then go on to observe that the Shannon index is simply the sum of the natural log of this value ($\ln(E)$) and the natural log of species richness ($\ln(S)$). (This assumes that natural logs have been used in the calculations.) It follows that the index can be decomposed into its two components:

$$H' = \ln S + \ln E$$

The most obvious advantage of this decomposition is that it allows the user to interpret changes in diversity. Thus, an ecologist can attribute a

decrease in the diversity of a community following a pollution incident to a loss of richness or evenness, or a combination of these. SHE analysis can also shed light on the underlying species abundance distribution. The essence of SHE analysis is the relationship between S (species richness), H (diversity as measured by the Shannon index), and E (evenness). The manner in which this relationship changes as a function of sample size can be remarkably informative. Like the estimation of species richness, this approach makes use of accumulated samples. Hayek and Buzas (1997) point out that when a sample of large and small N are compared, five scenarios are possible. Two of these are unlikely to prevail in natural communities but the remaining three are indicative of specific species abundance distributions.

1 $S_1 = S_2, H_1 = H_2, E_1 = E_2$; identical richness, evenness, and relative abundance of species irrespective of sample size.

2 $S_1 = S_2, H_1 \neq H_2, E_1 \neq E_2$; species richness remains constant but evenness changes.

3 $S_1 \neq S_2, H_1 = H_2, E_1 \neq E_2$; H remains constant because changes in S and E offset one another.

4 $S_1 \neq S_2, H_1 \neq H_2, E_1 = E_2$; E remains constant but S, and therefore H, changes.

5 $S_1 \neq S_2, H_1 \neq H_2, E_1 \neq E_2$; H changes because differences in S and E do not offset one another.

Scenarios 1 and 2 are implausible in nature partly because increased sampling almost always uncovers additional species; Hayek and Buzas (1997) explain why. However, scenario 3 indicates a log series distribution, scenario 4 a broken stick, and scenario 5 a log normal one. This means that a graphic method (SHE analysis) can potentially be used to distinguish the three patterns (though further exploration is required to rule out the possibility that other distributions could generate similar outcomes). Hayek and Buzas (1997) provide an example of this (Figure 4.3). I tested the approach using ground flora data collected for an Irish woodland. If the data are displayed in the form of a conventional species abundance plot a log normal distribution is revealed (Figure 4.4a); SHE analysis (Figure 4.4b) also indicates that the data are log normal in character. In this instance SHE analysis proved to be an effective method of deducing the underlying species abundance distribution, thus removing the need to formally fit the models and perform goodness of fit tests. However, although it is a promising method, SHE analysis needs wider testing across a range of taxa and communities. What, for example, will happen when truncated or left-skewed log normal distributions are observed? Its behavior in relation to abundance distributions other than the three discussed here also needs examination. Moreover, as Chapter 2 illustrated, distinguishing statistical models is not always an easy task. Interpreting the results of a SHE analysis could therefore be tricky.

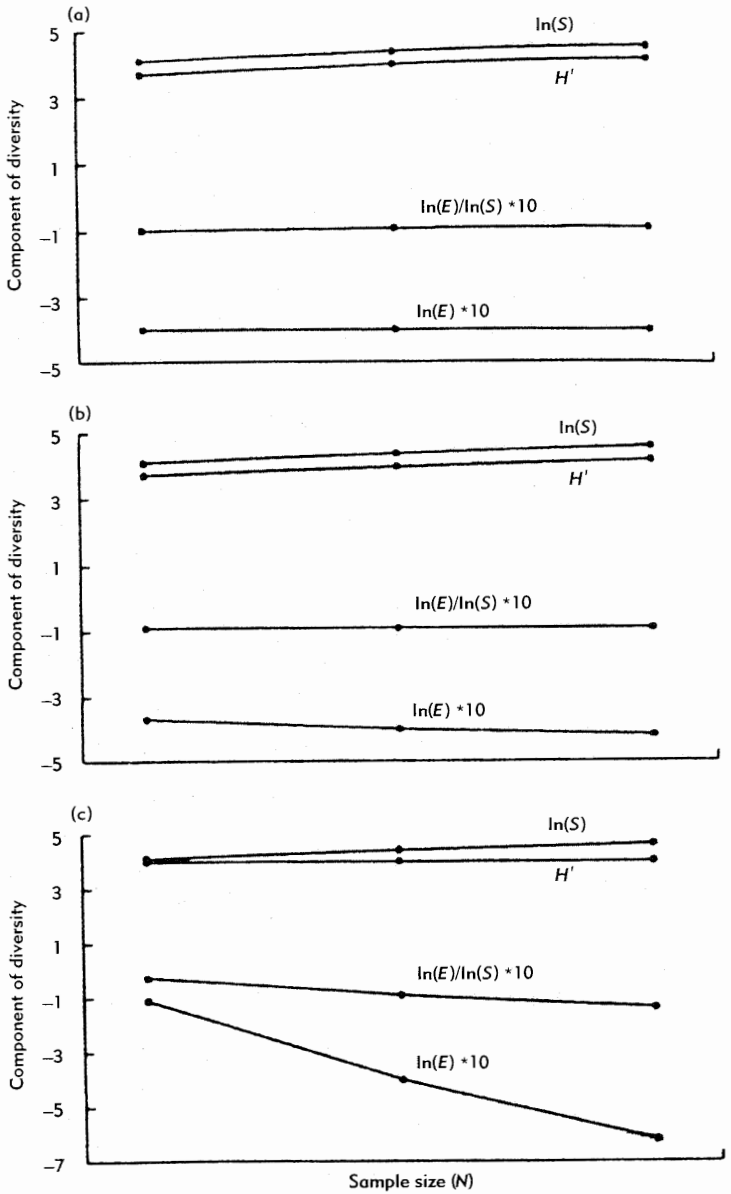

Figure 4.3 SHE analysis plots showing expected patterns for (a) broken stick, (b) log normal, and (c) log series distributions in relation to increasing N. Both $\ln(E)/\ln(S)$ and $\ln(E)$ are multiplied by 10. In the broken stick both S and H' are expected to increase and E to stay constant. The log normal is associated with an increase in S and H' but a decline in E. With the log series S will increase, H' will remain constant, and E will decrease. (Redrawn with permission from Hayek & Buzas 1997.)

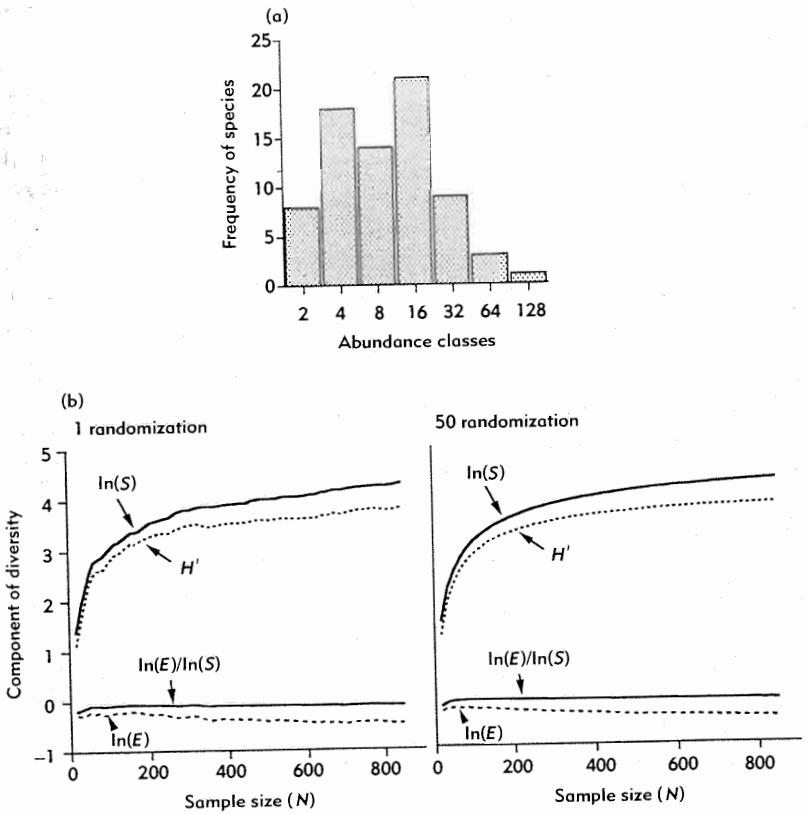

Figure 4.4 (a) The distribution of abundance of ground vegetation in an Irish woodland (Roe Valley, Co. Derry) is log normal. (b) SHE analysis correctly identifies this pattern. The two SHE graphs, which follow the format of Figure 4.3, plot ln(*S*), *H'*, ln(*E*)/ln(*S*) and ln(*E*) in relation to *N*. The values of *S*, *H'*, and *E* are based on one or 50 randomizations of 50 point quadrats; a "hit" by the pin of a quadrat represents $N = 1$. Both *S* and *H'* increase in relation to *N*, while, as predicted, *E* declines. These graphs also illustrate the consequences of multiple randomizations of data: the right panel, based on 50 randomizations, generates a smoother pattern than the left panel, which is based on one randomization.

Arita and Figueroa (1999) used SHE to examine geographic patterns of body mass diversity in Mexican mammals. They substituted the number of body mass categories for *S* and calculated p_i as the proportion of species per category rather than the usual proportion of individuals per species. The authors concluded that evenness (of the distribution of body mass values) was high at intermediate spatial scales but low at the regional one. This is a novel application of the SHE approach, but since no other evenness measures were considered it is unclear whether it is more informative than the alternatives. Buzas and Hayek (1998) describe how SHE can be used to identify communities (of Foraminifera in their example) along a gradient.

The Brillouin index

When the randomness of a sample cannot be guaranteed, for example during light trapping where different species of insect are differentially attracted to the stimulus (Southwood & Henderson 2000), or if the community is completely censused and every individual accounted for, the Brillouin index (HB), is the appropriate form of the information index (Pielou 1969, 1975). It is calculated as follows:

$$\mathrm{HB} = \frac{\ln N! - \sum \ln n_i!}{N}$$

and again rarely exceeds 4.5. Both the Shannon and Brillouin indices give similar and often correlated estimates of diversity. However, when the two indices are used to measure the diversity of a particular data set, the Brillouin index will always produce the lower value. This is because the Brillouin index describes a known collection about which there is no uncertainty. The Shannon index, by contrast, must estimate the diversity of the unsampled as well as the sampled portion of the community.

Evenness (*E*) for the Brillouin diversity index is obtained from:

$$E = \mathrm{HB}/\mathrm{HB}_{\max}$$

where $\mathrm{HB}_{\max}$ is calculated as:

$$\mathrm{HB}_{\max} = \frac{1}{N} \ln \frac{N!}{\{[N/S]!\}^{S-r} \cdot \{([N/S]+1)!\}^{r}}$$

where $[N/S]$ = the integer of N/S; and $r = N - S\,[N/S]$.

An important difference between the two measures of diversity is that the Shannon index will always provide the same answer so long as the number of species, and their proportional abundances, are held constant. Thus, if one site has 10 species each with five individuals and another site has 10 species each with 10 individuals, the Shannon index would return a value of 2.30 in both cases. The value of the Brillouin index, by contrast, would be 2.01 in the site with 50 individuals and 2.13 in the site with 100 individuals.

Since the Brillouin index measures the diversity of a collection, as opposed to a sample, each value of HB will, by definition, be different from

every other. This means that the index has no variance and that no statistical tests are needed to demonstrate significant differences. It is, of course, possible to use the jackknife or bootstrap procedure to generate a mean estimate along with an associated variance but whether such figures have any real meaning is open to debate. Laxton (1978) concludes that the Brillouin index is, mathematically speaking, the superior of the two information measures of diversity. Pielou (1969, 1975) strongly advocates its use in all circumstances where a collection is made, or samples are nonrandom, or where the full composition of the community is known. In practice, however, few ecologists take this advice as the Brillouin index is more time consuming to calculate, and less familiar, than the Shannon index. Its dependence on sample size can also sometimes lead to unexpected results, though admittedly only when there is a highly unusual species abundance distribution or when N (number of individuals) is low. The index cannot be used when abundance is measured as biomass or productivity (Legendre & Legendre 1983; Krebs 1999). The Brillouin index seems to suffer from many of the disadvantages of information statistics and offer few of the benefits. Notwithstanding this, it continues to be used often (Lo *et al.* 1998; Dans *et al.* 1999; Ito & Imai 2000), but not invariably (Andres & Witman 1995; Bartsch *et al.* 1998), to describe parasite assemblages.

Dominance and evenness measures

The information statistics described above tend to emphasize the species richness component of diversity. Another group of diversity indices are weighted by abundances of the commonest species and are usually referred to as either dominance or evenness measures (dominance and evenness being, of course, opposite sides of the same coin). One of the best known, and earliest, dominance measures is the Simpson index. It is occasionally called the Yule index since it resembles the measure G. U. Yule devised to characterize the vocabulary used by different authors (Southwood & Henderson 2000).

Simpson's index (D)

Simpson (1949) gave the probability of any two individuals drawn at random from an infinitely large community belonging to the same species as:

$$D = \sum p_i^2$$

where p_i = the proportion of individuals in the ith species. The form of the index appropriate for a finite community is:

$$D = \sum \left(\frac{n_i[n_i - 1]}{N[N-1]} \right)$$

where n_i = the number of individuals in the ith species; and N = the total number of individuals. Worked example 7 provides details.

As D increases, diversity decreases. Simpson's index is therefore usually expressed as $1 - D$ or $1/D$. Simpsons's index is heavily weighted towards the most abundant species in the sample, while being less sensitive to species richness. May (1975) has shown that once the number of species exceeds 10, the underlying species abundance distribution is important in determining whether the index has a high or low value. Confidence limits can be applied by jackknifing (Chapter 5).

The Simpson index is one of the most meaningful and robust diversity measures available. In essence it captures the variance of the species abundance distribution. Thus, when expressed as the complement ($1 - D$) or reciprocal ($1/D$) of D, the value of the measure will rise as the assemblage becomes more even. Although the reciprocal ($1/D$) is the most widely used form of the Simpson index, Rosenzweig (1995) notes that it can have severe variance problems, and recommends instead $-\ln(D)$, a transformation introduced by Pielou (1975) following the advice of C. D. Kemp. Rosenzweig (1995) advises that Kemp's transformation is easily interpretable, that it will reflect underlying diversity, and that it is independent of sample size. Lande (1996) observes that the overall diversity of a set of communities, measured as $1/D$, may be less than the average diversity of those communities—a conceptually intriguing notion—and recommends $1 - D$.

As noted in the previous chapter, Lande *et al.* (2000) find the Simpson index more effective than species accumulation curves in ranking communities. May (1975) approves of the measure because it is intuitively meaningful. Its utility has been illustrated in a range of contexts: see, for example, Itô (1997), Azuma *et al.* (1997), and Gimaret-Carpentier *et al.* (1998). Clarke and Warwick's (1998) index of taxonomic distinctness (discussed on p. 123) is a natural extension of Simpson's index. Lande (1996) demonstrates how the index can be partitioned to give a measure of diversity among, as well as within, assemblages, and describes how analysis of variance can be used to accurately estimate the total diversity in a region. Despite these plaudits, Simpson's index remains inexplicably less popular than the Shannon index.

Simpson's measure of evenness

Although Simpson's diversity measure emphasizes the dominance, as opposed to the richness, component of diversity, it is not strictly speak-

ing a pure evenness measure. A separate measure of evenness can, however, be calculated by dividing the reciprocal form of the Simpson index by the number of species in the sample (Smith & Wilson 1996; Krebs 1999):

$$E_{1/D} = \frac{(1/D)}{S}$$

The measure ranges from 0 to 1 and is not sensitive to species richness. It is usually termed $E_{1/D}$ to denote the use of the reciprocal form of the index. Smith and Wilson (1996) note that $E_{1/D}$ is formally related to its parent index:

$$(1/D) = E_{1/D} \cdot S$$

Bulla (1994) asserted that any good evenness index becomes a heterogeneity measure if multiplied by S (but see Molinari (1996) for a criticism of this comment). The Simpson evenness index is relatively unusual in that this multiplication restores the standard measure of Simpson diversity (Smith & Wilson 1996). The Shannon index can also be decomposed in the same way and it was this property that Buzas and Hayek (1996) and Hayek and Buzas (1997) exploited in their SHE analysis (described above).

McIntosh's measure of diversity

McIntosh (1967) proposed that a community can be envisaged as a point in an S-dimensional hypervolume and that the Euclidean distance of the assemblage from its origin could be used as a measure of diversity. The distance is known as U and is calculated as:

$$U = \sqrt{\sum n_i^2}$$

The McIntosh U index is not formally a dominance index. However, a measure of diversity (D) or dominance that is independent of N can also be calculated:

$$D = \frac{N - U}{N - \sqrt{N}}$$

And a further evenness measure can be obtained from the formula (Pielou 1975):

$$E = \frac{N - U}{N - N/\sqrt{S}}$$

The Berger–Parker index (d)

The Berger–Parker index, d, is an intuitively simple dominance measure (Berger & Parker 1970; May 1975). It also has the virtue of being extremely easy to calculate. The Berger–Parker index expresses the proportional abundance of the most abundant species:

$$d = N_{max}/N$$

where N_{max} = the number of individuals in the most abundant species. Conceptually d can be regarded as equivalent to geometric series k since both measures describe the relative importance of the most dominant species in the assemblage. As with the Simpson index, the reciprocal form of the Berger–Parker index may be adopted so that an increase in the value of the index accompanies an increase in diversity and a reduction in dominance. The simplicity and biological significance of the index leads May (1975) to conclude that it is one of the most satisfactory diversity measures available. In large assemblages ($S > 100$), d is independent of S, but in smaller ones its value will tend to decline with increasing species richness (Figure 4.5). (See Worked example 7 for further details.)

With the exception of Heip's index these evenness and dominance measures were described in the first incarnation of this book (Magurran 1988). Several new measures have been introduced since it was written.

Nee, Harvey, and Cotgreave's evenness measure

Nee *et al.* (1992) proposed the slope (b) of a rank/abundance plot (in which the abundances had been log transformed)—see also Wilson (1991)—as an evenness measure.

The resulting measure:

$$E_{NHC} = b$$

falls between $-\infty$ and 0, where 0 is perfect evenness. This range of values makes the measure difficult to interpret. There are other problems with the measure as well: it is more properly a measure of diversity than of evenness and rather similar to Kempton and Taylor's (1976) Q statistic (Smith & Wilson 1996). Smith and Wilson (1996) therefore proposed a new form of the measure:

$$E_Q = -2/\pi \arctan(b')$$

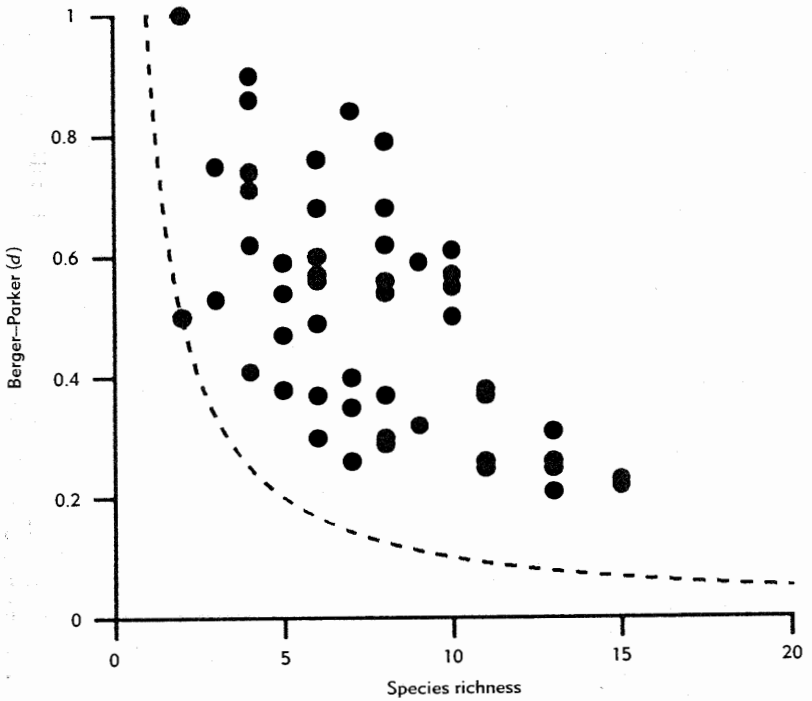

Figure 4.5 The relationship between the Berger–Parker index (d) and species richness (S) for freshwater fish assemblages in Trinidad. The dashed line indicates the value that d would take for a given number of species if all species were equally abundant (that is perfect evenness). Since d represents the proportional abundance of the most abundant species, lower values of d represent higher diversity. See text for details. (Redrawn with permission from Magurran & Phillip 2001b.)

In this measure the ranks are scaled before the regression is fitted. This is achieved by dividing all ranks by the maximum rank so that the most abundant species takes a rank of 1.0 and the least abundant a rank of $1/S$. The transformation ($-2/\pi$ arctan) places the measure in the 0 (no evenness) to 1 (perfect evenness) range.

Carmargo's evenness index

Carmargo (1993) also introduced an evenness measure:

$$E_C = 1 - \left(\sum_{i=1}^{S} \sum_{j=i+1}^{S} \left[\frac{p_i - p_j}{S} \right] \right)$$

where E_C = Carmargo's index of evenness; p_i = the proportion of species i in the sample; p_j = the proportion of species j in the sample; and S = the number of species in the sample.

Although the index is simple to calculate and relatively unaffected by rare species (Krebs 1989), Mouillot and Lepetre (1999) found it to be biased, especially in comparison with the Simpson index.

Smith and Wilson's evenness index

Smith and Wilson (1996) proposed a new index designed to provide an intuitive measure of evenness. This index measures the variance in species abundances, and divides this variance over log abundance to give proportional differences and to make the index independent of the units of measurement. Thus it does not matter, for example, whether biomass is measured in grams or kilograms, though, of course, different values will still ensue if abundance is measured in different ways (such as number of individuals versus biomass). The conversion by $-2/\pi$ arctan insures that the resulting measure falls between 0 (minimum evenness) and 1 (maximum evenness). Smith and Wilson called their measure E_{var}.

$$E_{var} = 1 - \left[\frac{2}{\pi \arctan\left\{ \left(\sum_{i=1}^{S} \left(\ln n_i - \sum_{j=1}^{S} \ln n_j / S \right)^2 \right) / S \right\}} \right]$$

where n_i = the number of individuals in species i; n_j = the number of individuals in species j; and S = the total number of species.

Smith and Wilson's consumer's guide to evenness measures

It can be difficult to know which evenness index is best in which context. Smith and Wilson (1996) conducted an extensive set of evaluations of available measures using a range of criteria. These included four **requirements** (essential attributes) and 10 desirable **features** of measures. Their requirements were as follow:

1 The measure is independent of species richness.

2 The measure will decrease if the abundance of the least abundant species is reduced.

3 The measure will decrease if a very rare species is added to the community.

4 The measure is unaffected by the units used to measure it.

The additional 10 features were as follow:

1 The maximum value of the index is achieved when abundances are equal.

2 The maximum value is 1.0.

3 The minimum value is achieved when abundances are as unequal as possible.

4 The index shows a value close to its minimum when evenness is as low as is likely to occur in a natural community.

5 The minimum value is 0.

6 The minimum is attainable with any number of species.

7 The index returns an intermediate value for communities that would be intuitively considered of intermediate evenness.

8 The measure should respond in an intuitive way to changes in evenness.

9 The measure is symmetric with regard to rare and common species, that is as much weight is given to minor species as to very abundant ones.

10 A skewed distribution of abundances should result in a lower value of the index.

Their results are summarized (for the measures described in this chapter) in Table 4.1. Smith and Wilson found that different indices often produced strikingly different results. For example, when asked to assess the evenness of a community in which the species abundances were 1,000, 1,000, 1,000, 1,000, 1,000, and 1 the measures produced values ranging from 0.046 to 0.999 (on a 0 to 1 scale). However, some measures did emerge as being significantly better than their competitors. Independence from species richness was Smith and Wilson's (1996) primary criterion. This was satisfied by $E_{1/D}$ (the Simpson evenness measure), a measure that also responded in an intuitive way to changes in evenness (feature 8 above, named by Smith and Wilson (1996) as the Molinari test after Molinari (1989)). Carmargo's index, E_C (Smith & Wilson 1996), the new index E_{var}, and their modification of Nee *et al.*'s (1992) index, E_Q, also met the species richness criterion and demonstrated other desirable properties. Smith and Wilson (1996) concluded with the following recommendations.

Table 4.1 A summary of Smith and Wilson's (1996) evaluation of evenness measures.

	Requirements				Features									
Index	1	2	3	4	1	2	3	4	5	6	7	8	9	10
J'	○	✓	✓	✓	✓	✓	✓	✓	✓	✓	✗	✓	✗	✓
E_{Heip}	○	✓	✓	✓	✓	✓	✓	✓	✓	✓	○	✓	✗	✓
$E_{1/D}$	✓	✓	✓	✓	✓	✓	✓	✗	✓	✓	○	✓	✗	✓
E_{MCI}	✗	✓	✓	✓	✓	✓	✓	✓	✓	✓	✗	✓	✗	✓
E_C	✓	✓	✓	✓	✓	✓	✓	✗	✓	○	✓	○	✗	✓
E_{var}	✓	✓	✓	✓	✓	✓	✓	○	✓	✓	○	✓	✓	○
E_{NHC}	✗	✓	✓	✓	✓	○	✓	○	✗	✓	○	○	✓	○
E_Q	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	○	✗	✓	✓

✓ = good; ○ = poor; ✗ = fail.

Recommendations.

1 When symmetry between rare and abundant species (feature 9 above) is required (that is, where rare and abundant species should be weighted equally with regard to their influence on the evenness measure) select:

(a) $E_{1/D}$ if minimum evenness should be 0, or a good response to an intuitive gradient in evenness is essential; or

(b) E_C if intermediate values for intermediate levels of evenness are sought.

2 When symmetry between rare and abundant species is not required (that is, where common species receive a higher weighting than rare ones), select:

(a) E_Q if a good response to the intuitive evenness gradient is not required; or

(b) E_{var} if it is.

Overall, Smith and Wilson (1996) rate E_{var} as the most satisfactory evenness measure. It will be interesting to see if it is widely adopted in the future. On the other hand the sound performance of Simpson's $E_{1/D}$ and its unambiguous relationship with its parent heterogeneity index—which is itself an excellent measure of diversity—are important recommendations.

Taxonomic diversity

If two assemblages have identical numbers of species and equivalent patterns of species abundance, but differ in the diversity of taxa to which the species belong, it seems intuitively appropriate that the most taxonomically varied assemblage is the more diverse (Figure 4.6). Moreover, measures of taxonomic diversity can be used in conjunction with species richness and rarity scores in the context of conservation (Virolainen *et al.* (1998) provide an example). The quest for measures that incorporate phylogenetic information can be traced back to Pielou (1975), who pointed out that diversity will be higher in a community in which species are divided amongst many genera as opposed to one where the majority of species belong to the same genus. The approach has gained impetus in the last decade as a consequence of their perceived role in setting conservation priorities (Vane-Wright *et al.* 1991; Williams *et al.* 1991;

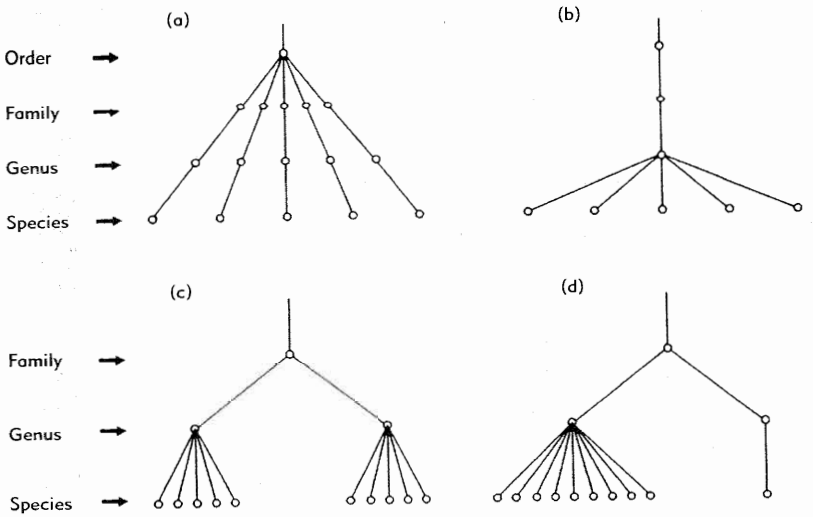

Figure 4.6 Taxonomic distinctness (Δ^+) is based on the average pairwise path lengths between species in an assemblage (see text for details). In this example (based on presence/absence data and ignoring species abundances) Δ^+ values are: (a) 3.0; (b) 1.0; (c) 1.56; and (d) 1.2. The four hypothetical assemblages are therefore ranked in an intuitive way. In other words, the greater the distribution of species amongst higher taxa, the greater the value of the index. (Redrawn with permission from Clarke & Warwick 1998.)

Vane-Wright 1996; Williams 1996). A further potential application in environmental monitoring has also been addressed (Warwick & Clarke 1995; Clarke & Warwick 1998, 1999; see also Chapter 5).

As long as the phylogeny of the assemblage of interest is reasonably well resolved, measures of taxonomic (or hierarchical) diversity are, in principle, possible.[4] Pielou (1975) adapted the Shannon index to include familial, generic, and species diversity and showed how the idea could be extended to the Brillouin index. Izsák and Papp (2000) and Ricotta (2002) describe how a taxonomic weighting factor can be incorporated into various diversity measures. May (1990b), Vane-Wright *et al.* (1991), and Williams *et al.* (1991, 1994) used a different approach and devised methods based on the topology of a phylogenetic tree. Information on taxonomic diversity can also be gleaned by summing the branch lengths within a taxonomic tree, as in Faith's (1992, 1994) measure of phylogenetic diversity (PD).[5]

Measures of taxonomic diversity are not spared the conceptual or practical problems of their species diversity counterparts. Both sets of measures give a predetermined weighting to the richness and evenness components of diversity. Sometimes this weighting can lead to a loss of information. For example, because Faith's PD measure reflects the cumulative branch length of the whole tree, it emphasizes the taxonomic richness of a set of organisms at the expense of its evenness (Clarke & Warwick 1998). This could hinder the identification of vulnerable assemblages (such as $2d$). Another consideration is sensitivity to sampling effort—a problem that species, and taxonomic, richness measures are particularly vulnerable to. Two recent developments—a taxonomic distinctness measure (Clarke & Warwick 1998; Warwick & Clarke 1998) and a functional diversity measure (Petchey & Gaston 2002a, 2002b)—merit further consideration.

4 The phylomatic website is a data base for applied phylogenetics and offers a different, but practical, approach to the phylogenetic measurement of diversity (http://www.phylodiversity.net/phylomatic/).

5 The PRIMER package calculates PD (www.pml.ac.uk/primer/index.htm).

Clarke and Warwick's taxonomic distinctness index

A very promising recruit to this suite of methods is Clarke and Warwick's taxonomic distinctness measure (Warwick & Clarke 1995, 1998, 2001; Clarke & Warwick 1998, 1999). (Webb (2000) has independently derived a very similar index for rain forest trees.)

A particular virtue of this measure, which is a natural extension of Simpson's index, is its robustness in the face of variable or uncontrolled sampling effort. Taxonomic evenness of an assemblage is also accounted for. Warwick and Clarke (2001) highlight the distinction between their **taxonomic distinctness** measure, which summarizes the pattern of relatedness in a sample, and **taxonomic distinctiveness** (the phylogenetic diversity of May, Vane-Wright, Williams, and Faith described above), which is used primarily to identify species of particular conservation importance.

The Clarke and Warwick measure, which describes the average taxonomic distance—simply the "path length" between two randomly chosen organisms through the phylogeny (or Linnean taxonomy) of all the species in an assemblage—has two forms. The first form, Δ or "taxonomic diversity" (appropriate for species abundance data), takes account of species abundances as well as taxonomic relatedness. It measures the average path length between two randomly chosen individuals (which may belong to the same species). The second form, Δ^* or "taxonomic distinctness," represents the special case where each individual is drawn from a different species. Δ^*, a pure measure of taxonomic relatedness, is equivalent to dividing Δ by the value it would take if all species belonged to the same genus, that is in the absence of a taxonomic hierarchy. When presence/absence data are used both measures reduce to the same statistic, Δ^+, which is the average taxonomic distance between two randomly selected species. It is calculated as follows:

Table 4.2 The weightings of steps in a taxonomic hierarchy for UK marine nematodes, standardized using taxon richness at each level (from Clarke & Warwick 1999).

k (step length)	Taxon	s_k (taxon richness)	ω_k (default weighing for constant step length)	$\omega_k^{(0)}$ (step length proportional to percentage decrease in richness)
1	Species	395	16.7	15.9
2	Genus	170	33.3	37.3
3	Family	39	50.0	60.2
4	Suborder	7	66.7	72.2
5	Order	4	83.3	86.1
6	Subclass	2	100	100

$$\Delta^+ = \left[\sum\sum_{i<j} \omega_{ij}\right] / \left[s\left(s^{-1}\right)/2\right]$$

where s = the number of species in the study; and ω_{ij} = the taxonomic path length between species i and j.

An important consideration is the weighting (v) assigned to each of the levels in the taxonomic hierarchy. The simplest approach, as used by Warwick and Clarke (1995, 1998) and Clarke and Warwick (1998), in their studies of marine nematodes, it to set the value of v as 1. Each step up through the hierarchy in search of a shared taxonomic level (from species to genera, families, suborders, orders, subclasses, and classes) increments the value of ω by 1. For instance, the path length for two species in the same genus is $\omega = 1$. As pairs of species become more distantly related the scores increase. If the species belong to the same family (but not genus) $\omega = 2$; if they share no more affinity than being members of the same class, $\omega = 6$.

As Clarke and Warwick (1999) recognize, there are cases where it may be inappropriate to treat v as a constant. This will arise if some taxonomic groupings convey little or no additional information. To resolve this problem, Clarke and Warwick (1999) suggest defining the weight of a step as proportional to the percentage of taxon richness accounted for by the step. This is illustrated in Table 4.2. Such scaling of richness weighting insures that the inclusion of a redundant taxonomic subdivison in the analysis cannot alter the value of Δ^+.

Rogers *et al.* (1999) contrasted the default weighting and the weighting based on taxon richness (ω_k and $\omega_k^{(0)}$) in their analysis of fish communities in the northeast Atlantic and found that they produced highly correlated values of Δ^+. Clarke and Warwick (1999) also analyzed different weightings and concluded that their measure of taxonomic distinctness is robust as long as the distinction between taxonomic levels is preserved.

Thus, although it may appear logical to adjust the weighting of ω in line with the distribution of phylogenetic diversity, unless the circumstances are exceptional the advantages of these extra calculations seem rather slight. Furthermore, because the weighting is based on the richness of a particular assemblage, comparisons across assemblages are problematic (Clarke & Warwick 1999).

As noted repeatedly in this book, one of the difficulties that frequently besets diversity measurement is sensitivity to sample size. Changes in sampling effort often have a dramatic impact on the value of the measure and the investigator is faced with the dilemma of trying to standardize sampling across sites or to sample each site exhaustively. A particular virtue of the taxonomic distinctness index is its lack of dependence on sampling effort (Price *et al.* 1999). This is dramatically illustrated in Figure 4.7, which contrasts the performance of three popular diversity statistics, the Shannon diversity, Margalef diversity, and Simpson diversity with Δ, Δ^*, and Δ^+. The issue of sample size is discussed in detail in the next chapter.

A further advantage of Δ^+ is that a significance test can be carried out. This examines the departure of Δ_m^+, the distinctness measure for a set of m species, from the value of Δ^+ calculated for the global species list, and has potential application in identifying impacted areas or localities of exceptional taxonomic richness. Clarke and Warwick (1998) derived the method and explain it in detail. Their starting assumption is that there is a reasonably complete inventory of species for a region—and, of course, that at least a Linnean taxonomy exists for these species. This condition is likely to be met for well-studied taxa, such as birds and mammals, in most parts of the world, and for less engaging organisms in the parts of the world well populated by taxonomists. The null hypothesis that the taxonomic distinctness of a locality is not significantly different from the global list is tested by repeatedly subsampling species lists of size m at random from the global list and constructing a histogram of the resulting estimates of Δ_m^+. The observed Δ_m^+ can be compared with the simulated values of Δ_m^+. To reject the null hypothesis at the 5% level, the observed Δ_m^+ should fall below the 2.5 percentile (i.e., below the 25th lowest out of 1,000 ranked simulated values of Δ_m^+) or above the 97.5 percentile (i.e., above the 975th out of 1,000 ranked simulated values) (Figure 4.8).

Since the simulation must be repeated for each locality with a different number of species (m) the procedure can be computationally demanding. However, a faster method is also available. This is based on the variance (equation 5 in Clarke and Warwick (1998); see also the equation on p. 126) of the subsample estimate which is then used to construct an approximate 95% confidence funnel (mean ± 2 s.d.) across the full range of m values (Figure 4.9). The mean is equal to the Δ^+ of

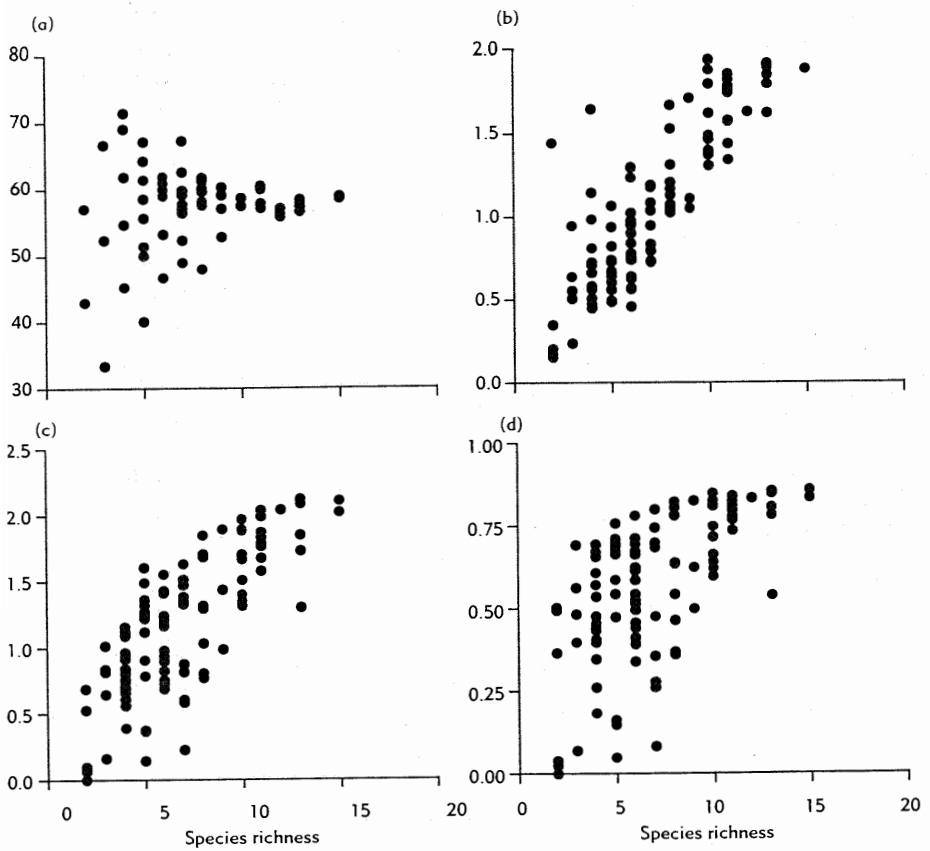

Figure 4.7 Unlike other popular diversity measures, for example the Margalef (b), Shannon (c), and Simpson (d) indices, Clarke and Warwick's taxonomic distinctness measures, such as average Δ^+ shown here in panel (a), are independent of species richness. Data shown represent Trinidadian freshwater fish assemblages and were collected by Phillip (1998).

the global list and the standard deviation is the square root of the variance expression:

$$\mathrm{var}(\Delta^+_m) = 2(s-m)[m(m-1)(s-2)(s-3)]^{-1} \left[(s-m-1)\sigma^2_\omega + 2(s-1)(m-2)\sigma^2_\varpi\right]$$

where s = the whole set of species; m = the number of species in the subset; ω_{ij} = the predetermined weightings; $\sigma_\omega^2 = [(\Sigma_i\Sigma_{j(\neq i)}\ \omega_{ij}^2)/s(s-1)] - \varpi^2$ (i.e., the variance of all the path lengths (ω_{ij}^2) between different species);

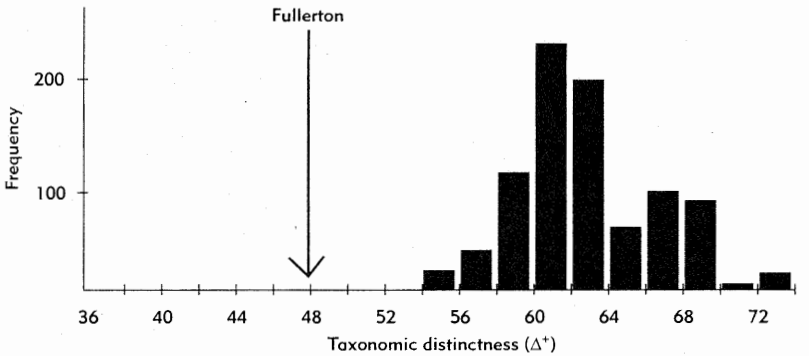

Figure 4.8 The Fullerton River in Trinidad has been colonized by tilapia (*Oreochromis niloticus*), one of the world's most invasive organisms (www.issg.org/database). Has this invasion had an impact on the taxonomic distinctness of the assemblage? The graph plots 999 simulated values of Δ^+, based on $m = 8$ species (the species richness of the Fullerton site) drawn at random from the Trinidad species pool. The value for Fullerton lies well below the 2.5 percentile indicating that the site is less taxonomically distinct than expected. The data are from Pillip (1998) and the analysis used the PRIMER package.

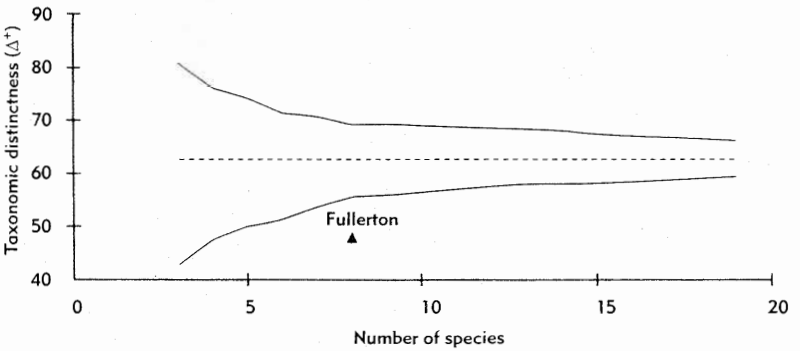

Figure 4.9 Confidence funnel indicating the taxonomic distinctness of the Fullerton site (see Figure 4.8) in relation to the pattern for localities across Trinidad. The funnel plot shows the 95% probability limits of Δ^+ (based on 999 random selections) for each value of m (number of species). The dotted line indicates average taxonomic distinctness which, as noted in the text, does not change with S. The points for the other sites are not shown on this graph for clarity but can be seen in Figure 4.7a. The data are from Phillip (1998) and the analysis used the PRIMER package.

$\sigma_\varpi^2 = [(\Sigma_i\varpi_i^2)/s] - \varpi^2$ (i.e., the variance of the mean path lengths (ϖ_i) from each species to all others); $\varpi_i = (\Sigma_{j(\neq i)}\omega_{ij})/(s-1)$; and $\varpi = (\Sigma_i\ \varpi_i)/s = (\Sigma_i\Sigma_{j(\neq i)}\omega_{ij})/[s(s-1)] \equiv \Delta^+$.

Since σ_ω^2 and σ_ϖ^2 are constants that are a function of the taxonomic structure of the global species list, they need only be calculated once to construct the confidence funnel.

Variation in taxonomic distinctness (Λ^+) (Clarke & Warwick 2001b; Warwick & Clarke 2001) measures the evenness with which the taxa are distributed across the hierarchical taxonomic tree. Λ^+ is largely independent of sample size and (as with Δ^+) can be tested against an expectation based on the species list for the region. It is also possible to construct a two-dimensional "envelope" plot of Δ^+ versus Λ^+. This combination provides a statistically robust summary of the taxonomic diversity of the assemblage. The PRIMER package[6] is recommended for all these analyses.

As Clarke and Warwick (1998) note, these tests, in contrast to virtually all other diversity statistics, can be used in situations where sampling is uncontrolled and where the data are in the form of species presence/absence. Indeed, they argue that the method is relatively robust against sampling inconsistencies, so long as these do not bias the estimates of Δ_m^+ in any systematic way. For example, recorders in different localities might vary in expertise but this will not matter if misidentifications occur at random across the species pool. Of course, certain groups are more taxonomically challenging and it is important that the user is vigilant for any potential biases. In addition, some sampling techniques, such as notoriously different types of light trap (Southwood & Henderson 2000), can favor the collection of some taxa and prejudice the recording of others (see also Chapter 5).

Functional diversity

Functional diversity has attracted considerable interest as a consequence of the current debate on ecosystem performance. Indeed, the positive relationship between ecosystem functioning and species richness is often attributed to the greater number of functional groups found in richer assemblages (Diaz & Cabido 1997; Tilman 1997, 2000; Hector *et al.* 1999; Chapin *et al.* 2000; Loreau *et al.* 2001; Tilman *et al.* 2001). Moreover, it is not always obvious how functional groups should be delineated, nor which species should be assigned to them. Petchey and Gaston (2002a, 2002b) have recently proposed a new method for quantifying functional diversity (FD). This approach is conceptually similar to the phylogenetic diversity (PD) measure of May (1990b), Vane-Wright *et al.* (1991), Faith (1992, 1994), and Williams *et al.* (1994). Both measures are based on total branch length. However, whereas phylogenetic diversity is estimated from a phylogenetic tree, functional diversity uses a dendrogram constructed from species trait values. One important consideration is that only those traits linked to the ecosystem process of interest

6 www.pml.ac.uk/primer/index.htm.

are used. Thus a study focusing on bird-mediated seed dispersal would exclude traits such as plumage color that are not related to this function. A trait matrix, consisting of s species and t traits is assembled, and then converted into a distance matrix. Standard clustering algorithms are used to generate a dendrogram, which in turn provides the information needed to calculate branch length (Petchey & Gaston 2002b). The resulting measure is continuous and can be standardized so that it falls between 0 and 1. The method makes intuitive sense. For example, a community with five species with different traits will have a higher FD than a community of equal richness but where the species are functionally similar. And, as the complementarity of the species increases, the value of FD becomes more strongly associated with species richness. In addition, the measure appears robust and provides qualitatively similar results when different distance measures and clustering techniques are used. FD has been shown to be a powerful technique for evaluating the functional consequences of species extinctions (Petchey & Gaston 2002a) and has the potential to shed light on a number of key issues in ecology, such as species packing and community saturation. To date it has been evaluated using well-censused assemblages in which the functional roles of the member species have been extensively documented. It will be interesting to see how it performs when samples are incomplete and where the functional dynamics are less well understood.

Body size and biological diversity

In contrast to taxonomic and functional diversity measures, "traditional" diversity measures treat all species as equal. Species abundances provide the only weighting in heterogeneity and evenness statistics. Other differences are ignored. Species abundance (typically measured as the number of individuals or biomass) is an intuitive measure of species importance. Indeed, niche apportionment models are built on the assumption that relative abundance is a surrogate for the manner in which resources are distributed amongst species (Chapter 2). None the less, species abundance data can be time consuming to collect. Oindo *et al.* (2001) have devised a new index which makes inferences about the relative abundances of species from their body size. It is based on the observation (Damuth 1981) that there is a predictable relationship between body size and abundance:

$$A = kW^{-0.75}$$

where A = the abundance of a species; and W = the average body mass of a species.

Different guilds have different values of k. Oindo *et al.*'s (2001) index uses this relationship to estimate diversity:

$$B = \sum_{i=1}^{n} w_i^{-0.75}$$

The new index performed well when tested using assemblages of mammalian herbivores in Kenya and has potential in rapid biodiversity assessment. Further evaluation would be useful, particularly in circumstances where species have been disproportionately harvested.

Summary

1 Diversity indices, sometimes referred to as heterogeneity measures, distil the information contained in a species abundance distribution into a single statistic. Heterogeneity measures fall into two categories: parametric indices, such as log series α, that are based on a parameter of a species abundance model, and nonparametric indices, such as the Simpson index, that make no assumptions about the underlying distribution of species abundances. Nonparametric measures can be further divided into those that emphasize the species richness component of diversity, for example the Shannon index, and those, for instance the Berger–Parker index, that focus on the dominance/evenness component.
2 Although nonparametric measures are not linked to specific species abundance models the underlying distribution of species abundances can influence their performance.
3 One of the most popular diversity statistics, the Shannon index, has properties that can impede the interpretation of results. On the other hand, the Simpson index performs well, both as a general purpose diversity statistic and when recast as an evenness measure. Advice on the selection of diversity measures is provided in Box 4.1.
4 Communities may be identical in terms of richness and evenness but differ in the taxonomic diversity of their species. A new class of measures takes this aspect of biological diversity into account. One promising method, the Warwick and Clarke taxonomic distinctness measure, is an extension of the Simpson index and has the advantage of being robust against variation in sampling effort.
5 Confidence limits can be applied to many of these measures. Chapter 5 provides details.

chapter five

Comparative studies of diversity[1]

As I noted in the introductory chapter, biodiversity measurement is fundamentally a comparative discipline. A single estimate of diversity is not informative. It is only when we ask whether forest x has more bird species than forest y or how pollution has affected the diversity of assemblage z that the measures begin to have meaning. Analyses of shifts in species richness along spatial or temporal gradients (such as latitude or succession) are one form of comparative investigation. Relating patterns of diversity to variation in land use is another. Even estimates of the total number of species on earth are comparative in the sense that they can be contrasted with levels of diversity at earlier points in evolutionary history, adopted as a benchmark against which extinction rates can be evaluated or used to highlight our planet's unique biota. Meaningful comparisons, however, demand good data. Since sampling effort has a significant impact on biodiversity measurement the chapter begins by discussing sampling procedures and pitfalls. The units in which abundance is measured—for example, number of individuals, biomass, and cover—are also discussed. I then review the statistical methods used to determine whether the diversity of two (or more) assemblages differ and to set confidence limits on diversity measures. The chapter concludes by focusing on the application of diversity measurement in environmental assessment.

1 After Sanders (1968).

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