chapter two

The commonness, and rarity, of species[1]

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.)
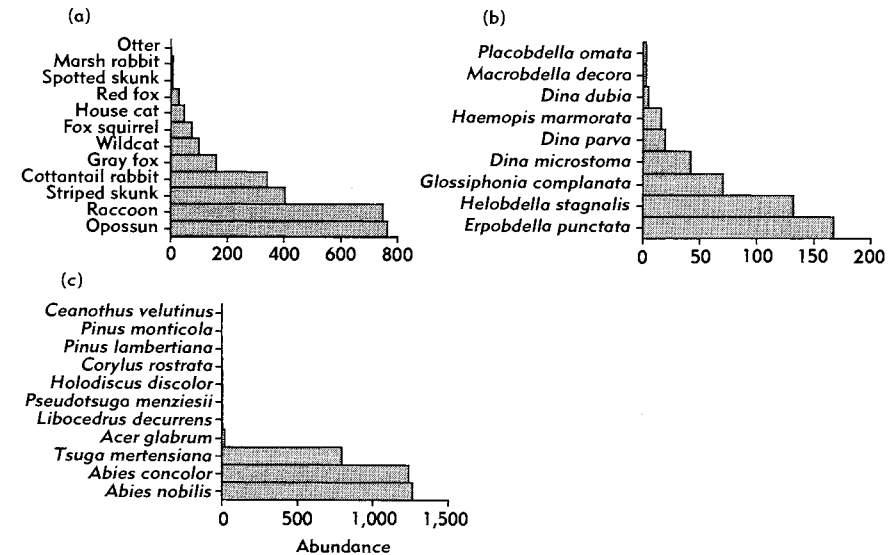
In no environment, whether tropical or temperate, terrestrial or aquatic, are all species equally common. Instead, it is universally the case that some are very abundant, others only moderately common, and the remainder—often the majority—rare. This pattern is repeated across taxonomic groups (Figure 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 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,
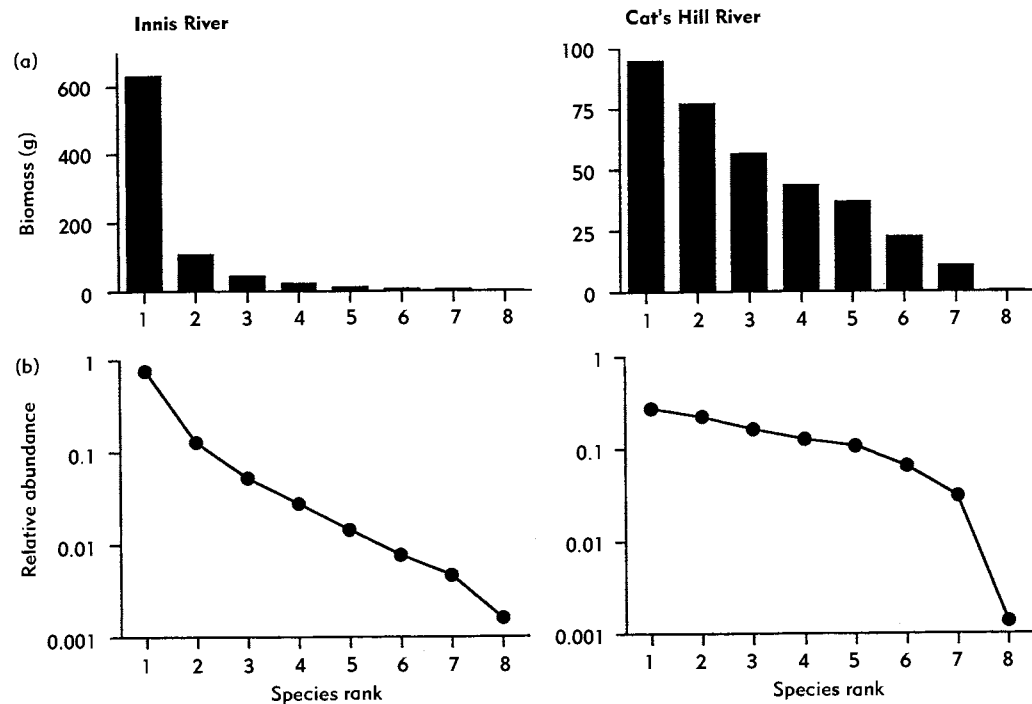
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1   After Preston (1948).
2   Lloyd and Ghelardi (1964) introduced the term "equitability" to mean the degree to which the relative abundance distribution approaches the broken stick distribution. It is not a synonym for evenness. Cotgreave and Harvey (1994) point out that the usual meaning of equitability is "resonableness."

Figure 2.2 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
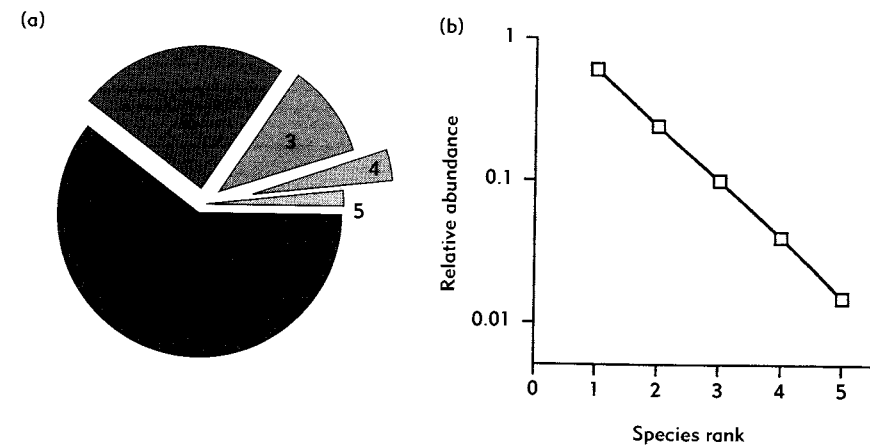

Figure 2.3 The relationship between niche apportionment and relative abundance. (a) Niche space (represented as a pie diagram) being successively carved up by five species each of which takes 0.6 of the remaining resources. Thus, species 1 pre-empts 0.6 of all resources, species 2 takes 0.6 of what is 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-
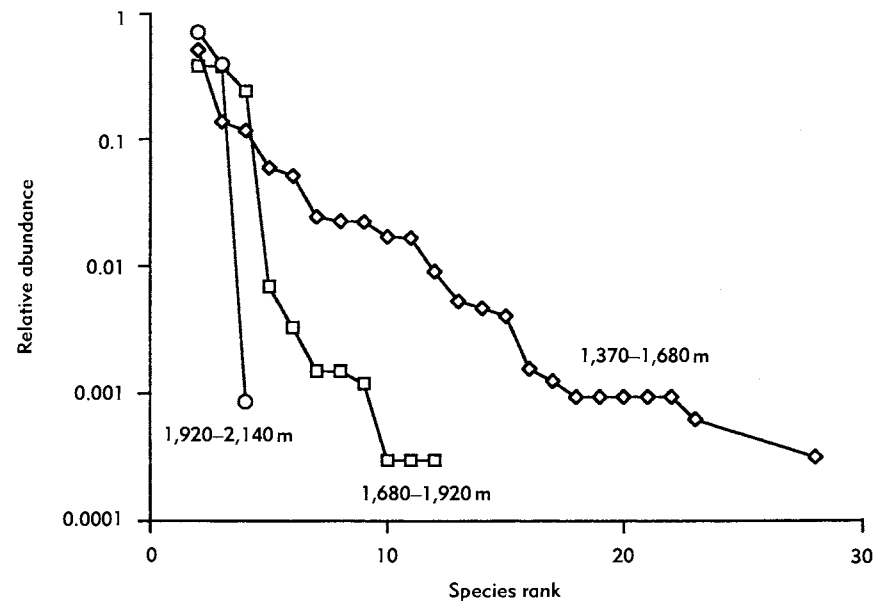
Figure 2.4 An example of a rank/abundance or Whittaker plot. The *y* axis shows the relative abundance of species (plotted using a $\log_{10}$ scale) while the *x* axis ranks each species in order from most to least abundant. The three lines show the densities of trees, in relation to elevation, on quartz 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
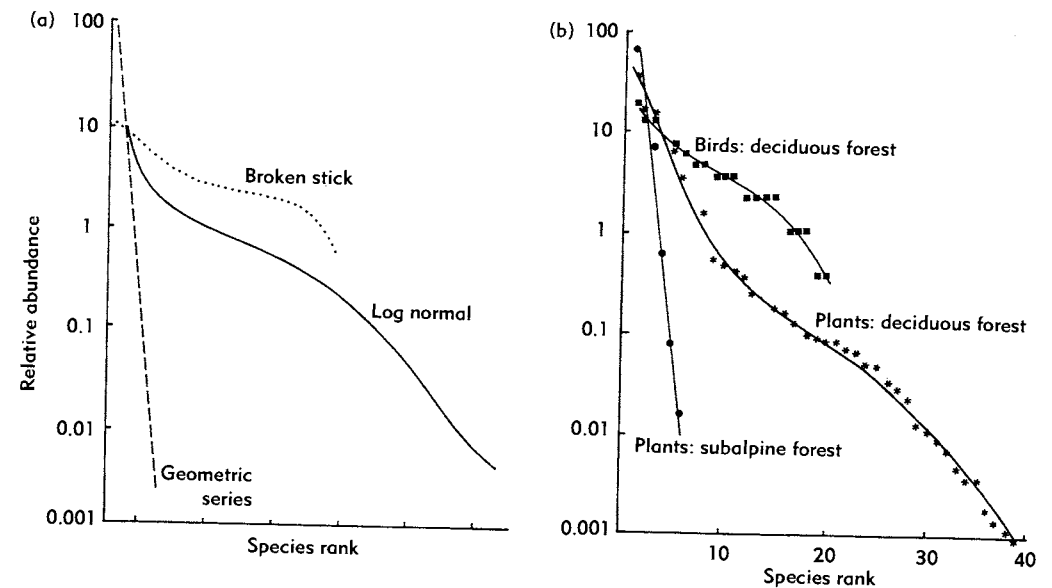
Figure 2.5 (a) Rank/abundance plots illustrating the typical shape of three well-known species abundance models: geometric series, log normal, and broken stick. (b) Empirical rank/abundance plots (after Whittaker 1970). The three assemblages are nesting birds in a deciduous forest, West Virginia, vascular 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.
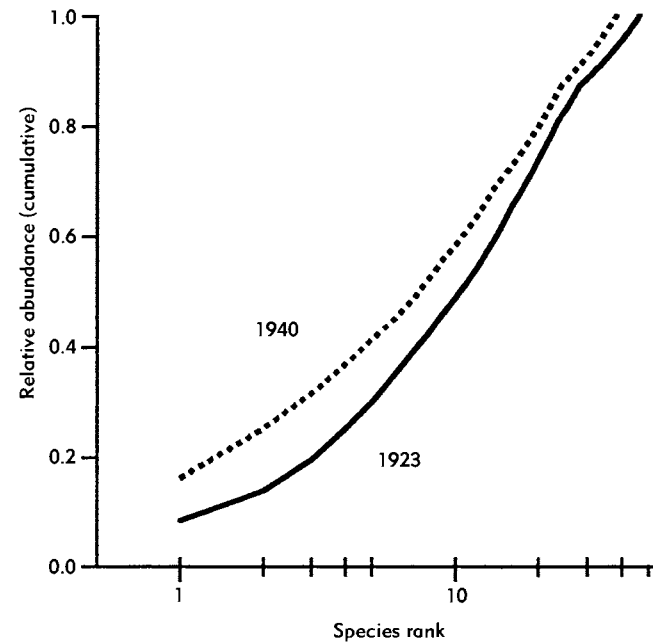
Figure 2.6 k-dominance plots for breeding birds at "Neotoma" (table II, Preston 1960). Censuses from 1923 and 1940 are compared. The latter plot is the more elevated, indicating that this assemblage is less diverse.


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. The 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.)

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).

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
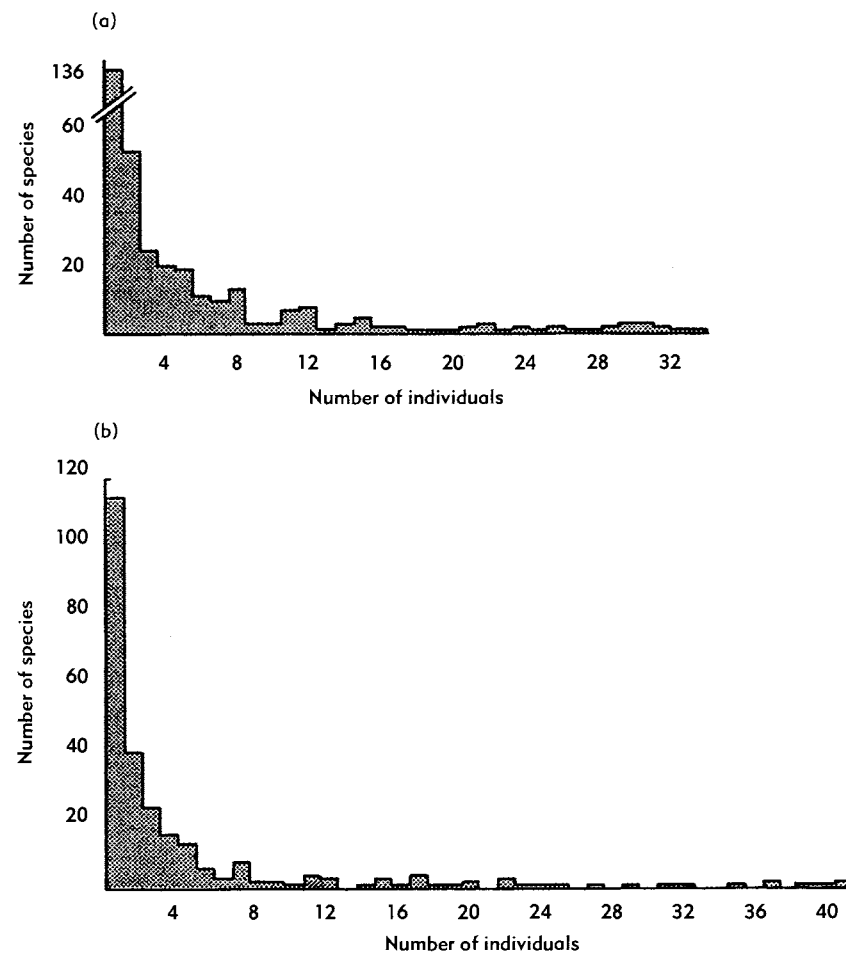
Figure 2.8 Frequency of species in relation to abundance. These graphs show the relationship between the number of species and the number of individuals in two assemblages: (a) freshwater algae in small ponds in northeastern Spain and (b) beetles found in the River Thames, UK. In both cases the mode 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.)

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.)

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 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:

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

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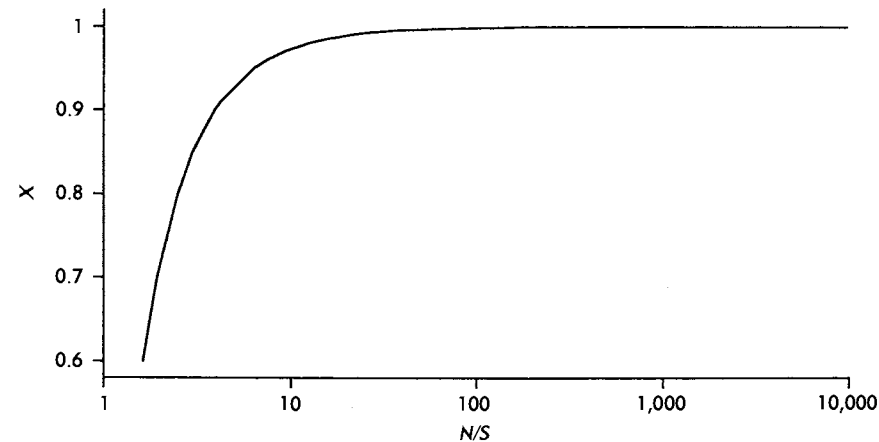
Figure 2.10 Values of x in relation to N/S. See text for details.

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:

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

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:

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

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
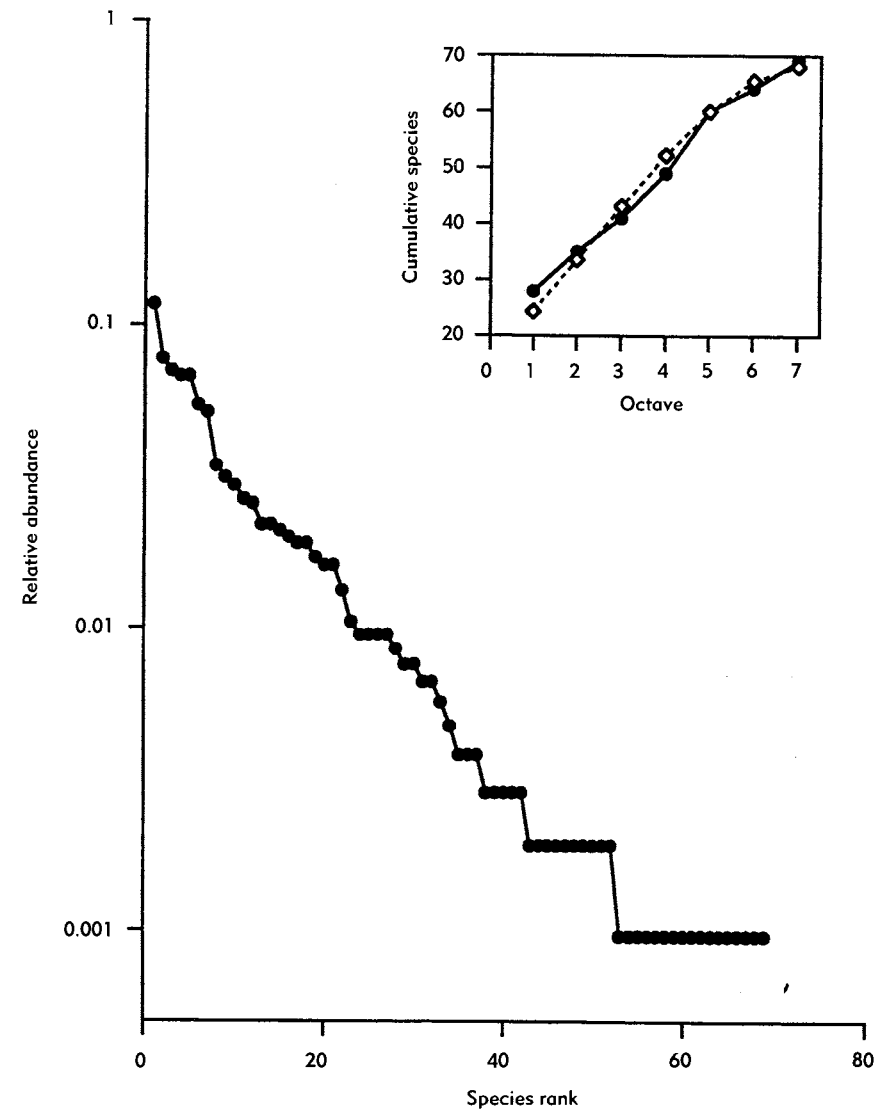
Figure 2.11 Rank/abundance plot of ground vegetation in an Irish conifer plantation. The slope of the graph is indicative of a log series distribution. The inset shows the cumulative observed (solid line) and expected (dotted line) number of species in relation to abundance class (in octaves) for the 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).
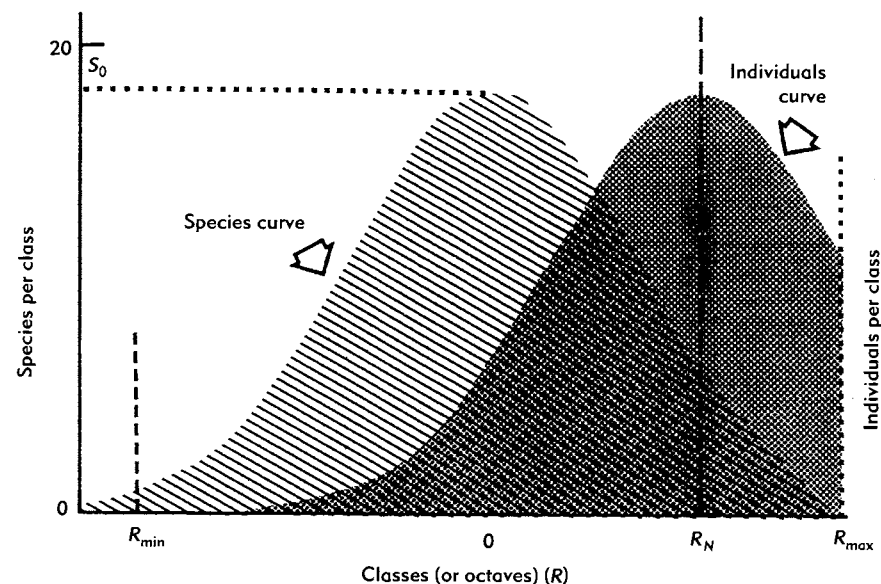
Figure 2.12 Features of the log normal distribution. The striped curve (species curve) shows the distribution of species amongst classes. If these classes are in $\log_2$ – that is doublings in numbers of individuals – they are referred to as octaves (see Figure 2.9). Since the distribution is symmetric, 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
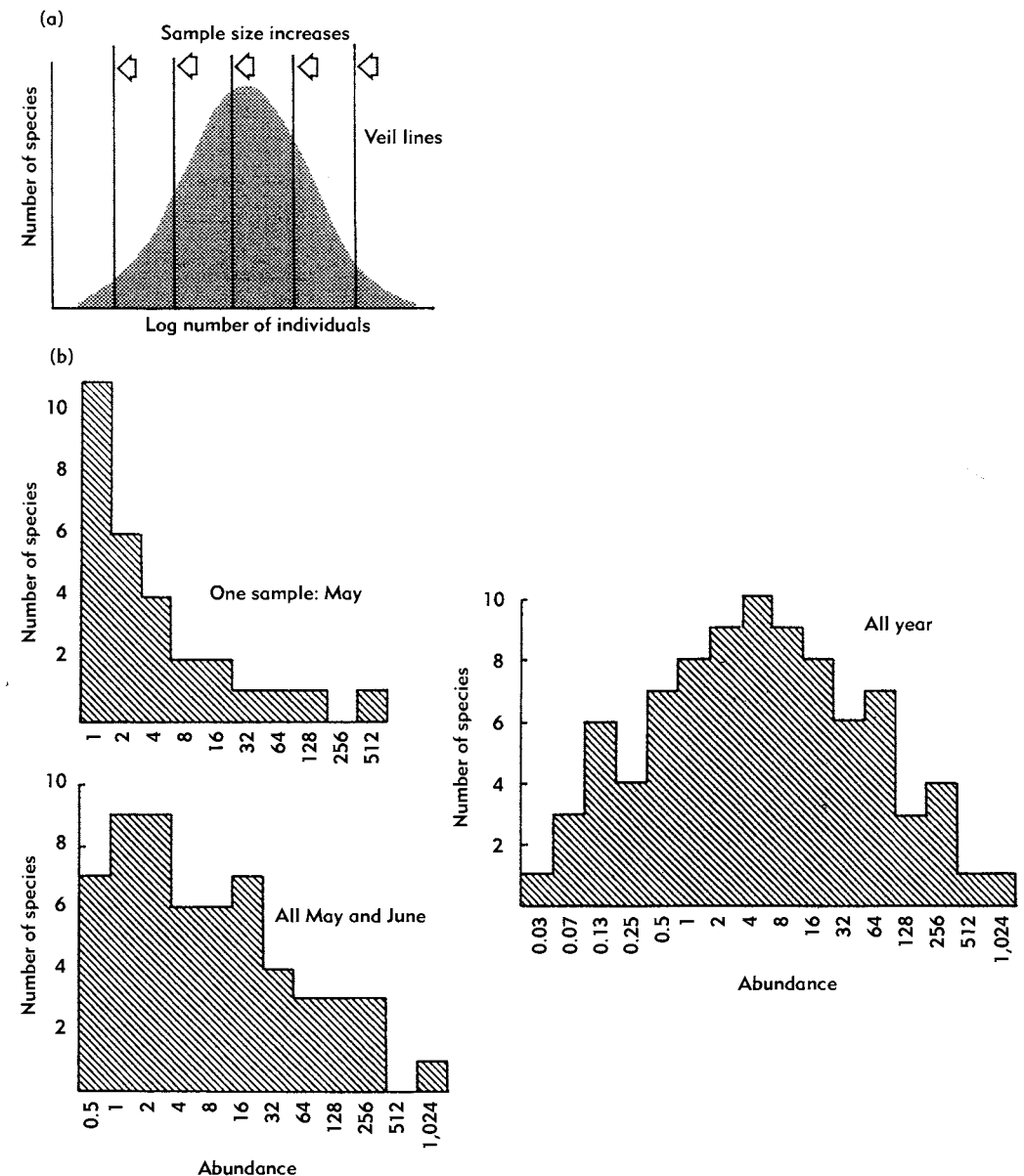
Figure 2.13 The veil line. (a) In small samples, only the portion of the distribution to the right of the mode may be apparent. However, as sample size increases the veil line is predicted to move to the left revealing first the mode and eventually the entire distribution. This effect is evident in (b). (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 1988.)

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

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[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^*:σ, 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
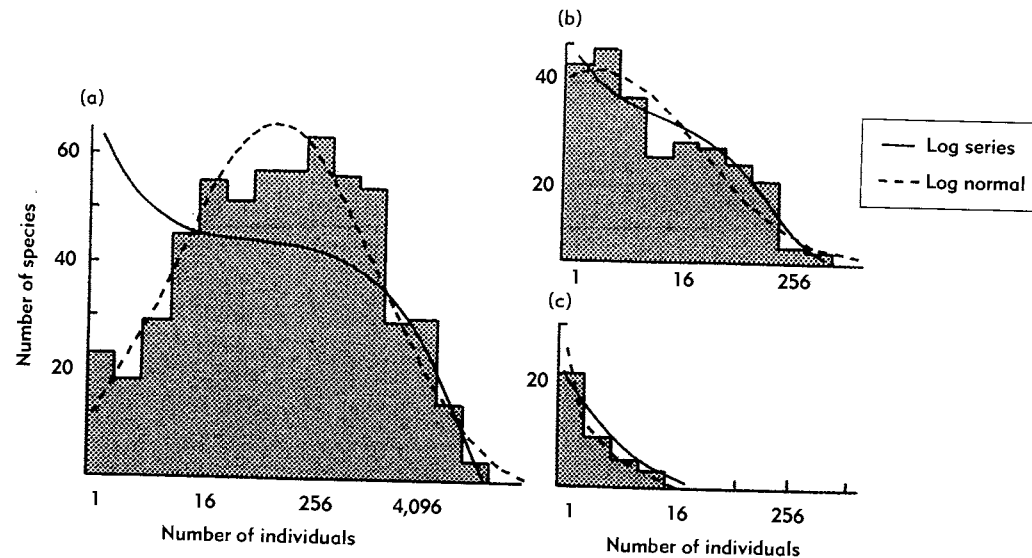
Figure 2.14 The relationship between log series and log normal distributions. These three graphs show: (a) the abundance of moths summed across 225 sites through Britain, (b) a typical annual sample from a single rural site, and (c) a sample from an impoverished urban site. The dashed lines represent 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-
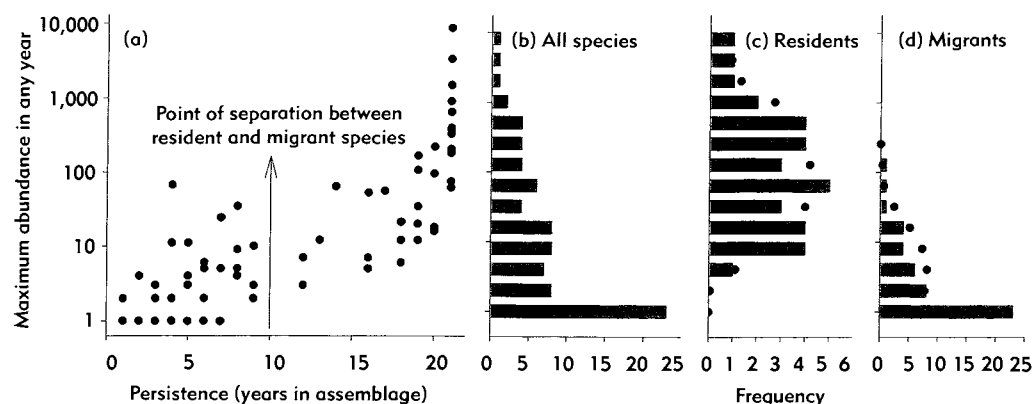
Figure 2.15 The pattern of abundance and persistence in a estuarine fish assemblage (Bristol Channel, UK). The data are for a 21-year time series of monthly samples. (a) The number of years in which each fish was observed, plotted against the maximum abundance in any one year. A discontinuity (indicated 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 lin-

guistics 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 $P \gg 0.05$, 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
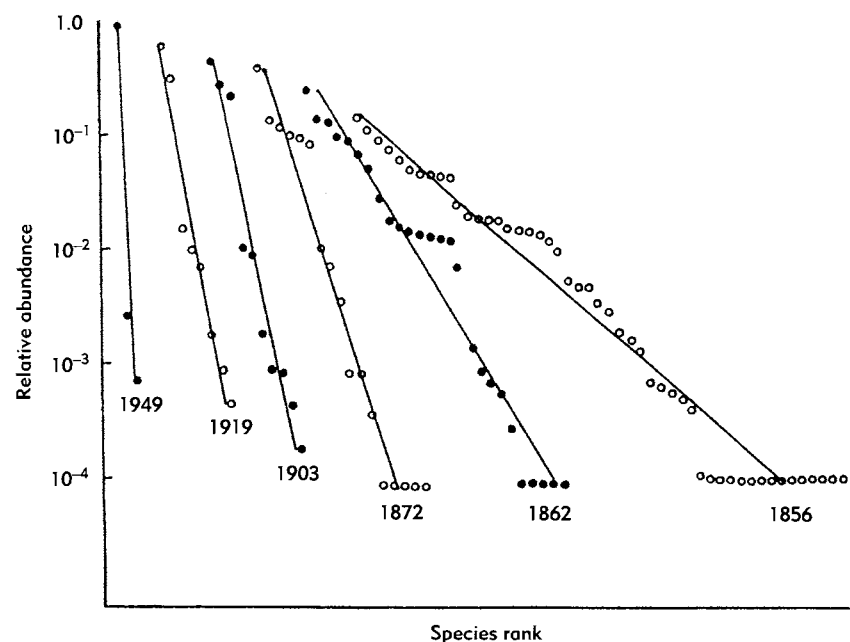
Figure 2.16 Changes in the relative abundance of plant species in the Rothamsted Park Grass Experiment over time. The grass has been subjected to continuous application of nitrogen fertilizer since 1856. (Redrawn with permission from Tokeshi 1993.)

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

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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

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.

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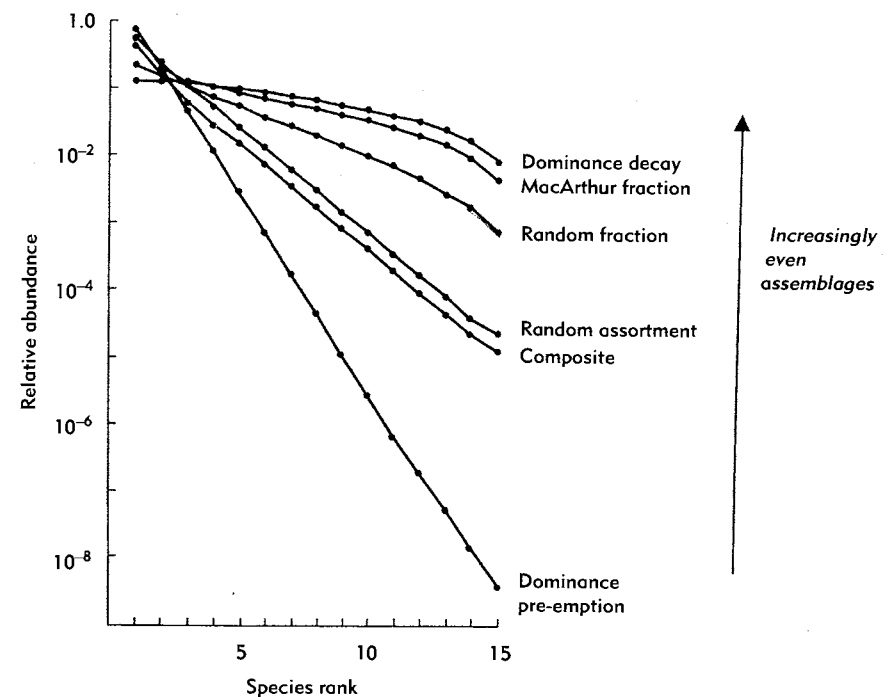
Figure 2.17 Pattern of relative abundance exhibited by a selection of Tokeshi's niche apportionment models. (Redrawn with permission from Tokeshi 1999.)

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 fresh-water 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.

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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 $\geq 41.4\%$ and $\leq 70.7\%$ 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.

Species	where $K = 0$		where $K = 0.5$		where $K = 1$	
	X	X^K	X	X^K	X	X^K
A	50	1	50	7.07	50	50
B	25	1	25	5	25	25
C	25	1	25	5	25	25
	$\equiv$ random fraction				$\equiv$ MacArthur fraction	

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-

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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 bio-diversity 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 Hen-

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

derson (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.

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.
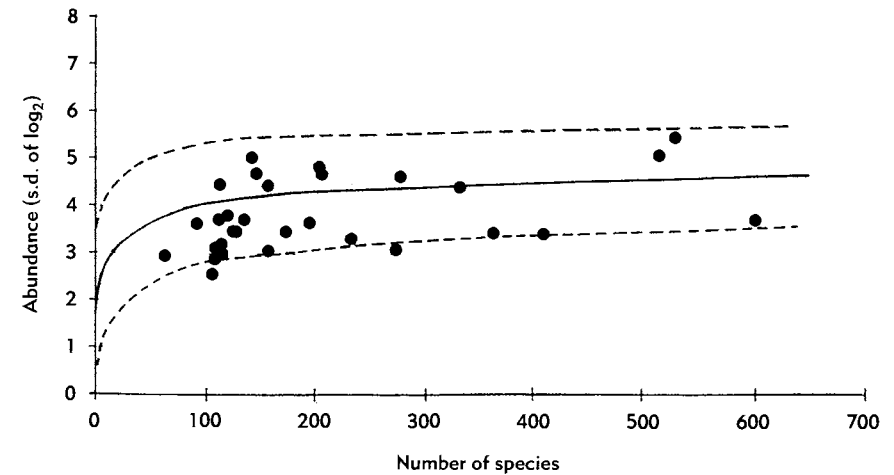
Figure 2.19 Testing the fit of a number of assemblages to a single model. Here a power fraction model with $k = 0.05$ is fitted to a series of species-rich assemblages. The solid line is the standard deviation of $\log_2$ abundance predicted by the model. Broken lines represent ± 2 s.d. of this standard 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 $\pm 95\%$ 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.
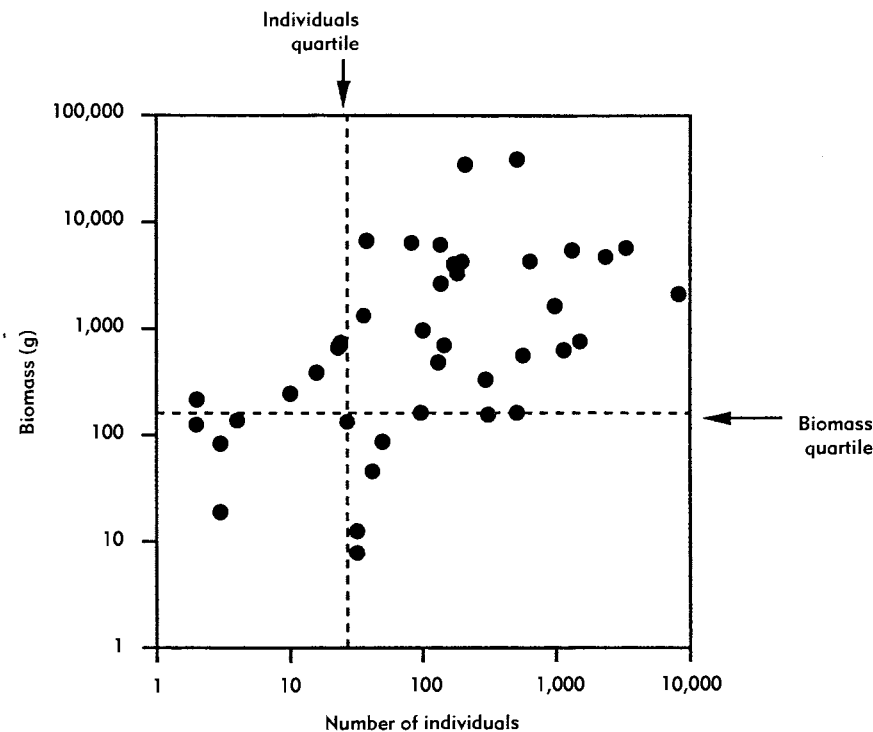
Figure 2.20 Rarity amongst freshwater fish in Trinidad and Tobago according to Gaston's quartile criterion. Fish abundance was measured in two ways – either as numbers of individuals or as biomass. Data were collected by Phillip (1998). The quartiles in the two distributions are shown as broken lines; 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).

Geographic 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).

Geographic 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.