1 What is rarity?

Discussions will soon be at cross-purposes if it is not clearly recognised that our concepts of what is rare will depend on the scale of our individual experience and on the range or narrowness of our special interests.

J.L. Harper (1981)

Rarity is one of those concepts that suffuses our culture: it defies precise definition and when used by the scientist it is often given a spurious accuracy to satisfy our need for precision.

V.H. Heywood (1988)

Population and community biology have repeatedly been plagued with problems of definition. The meaning of such fundamental terms and concepts as competition, density dependence, carrying capacity, niche, stability and community have all, and often for prolonged periods, been debated (e.g. Pimm, 1984; Giller and Gee, 1987; Murray, 1987; Dhondt, 1988; Keddy, 1989; Schoener, 1989). Such discussion of the use and interpretation both of words and concepts may, on occasion, degenerate into arguments over semantics. However, for any area of study, clarity of terminology is essential to the establishment of a rigorous framework in which both theoretical and empirical work can be placed. With regard to the study of rarity no general theory and no such framework presently exist. At the outset, therefore, we would do well to be clear about what we mean by rarity and rare species.

In this chapter the view of rarity upon which this book is founded is established, and its relation to a number of issues is explored. The first section identifies the variables by which rarity is defined, and the second how, on the basis of those variables, species which are rare can be recognized. The third and fourth sections address the relationships of spatial scale and endemism to concepts of rarity, and the following section considers how to delineate the assemblage with respect to which species are viewed as rare. The penultimate section is concerned with the interaction between rarity and vulnerability, and the concluding section outlines some further features of how rarity will be used in this book.

1.1 THE VARIABLES USED TO DEFINE RARITY

The term 'rare' has a variety of meanings in common usage (Table 1.1; Harper, 1981). However, in the context of population and community biology it is, by and large, used in a somewhat more constrained sense. Rare species are regarded as those having low abundance and/or small ranges. What is meant

Table 1.1 Extracts from The Shorter Oxford English Dictionary (1983) defining the term 'rare'

1	Having the constituent particles not closely packed together.
2	(a) Having the component parts widely set; of open construction; in open order. (b) Thinly attended or populated.
3	Placed or stationed at wide intervals; standing or keeping far apart.
4	Few in number and widely separated from each other (in space or time); forming a small and scattered class.
5	Of a kind, class, or description seldom found, met with, occurring; unusual, uncommon, exceptional.
6	Unusual in respect of some good quality; remarkably good or fine.

by this is unfortunately rather infrequently expressed. Usher (1986a) neatly captures the situation in describing rarity as 'an intuitive concept'. Indeed, while the magnitude of abundance and range size may serve as some lowest common denominator, there remains a bewildering diversity of viewpoints on the limits to what constitutes rarity in population and community biology (Mayr, 1963; Drury, 1974, 1980; Harper, 1981; Margules and Usher, 1981; Rabinowitz, 1981a; Reveal, 1981; Main, 1982; Cody, 1986; Fiedler, 1986; Rabinowitz *et al.*, 1986; Soulé, 1986; Usher, 1986a, b; Heywood, 1988; Ferrar, 1989; Hanski, 1991a; Fiedler and Ahouse, 1992; McCoy and Mushinsky, 1992; Reed, 1992). Habitat specificity, taxonomic distinctness, and persistence through ecological or evolutionary time, have variously been regarded either as additional variables by which rare species can be identified, or as restrictions upon which species with low abundances or small range sizes are regarded as rare. In many instances the resultant definitions serve to prejudge the causes of the phenomenon. Some of these definitions may be reconciled but many may not.

There are various possible ways to move forward from the present confused position. One approach would be to seek further variables that may be used to define rare species. However, this seems likely to generate more, rather than less, confusion. Here I have chosen to regard rarity as simply being the state of having a low abundance and/or a small range size. I seek to limit it on the basis of no additional variables. This follows Reveal's (1981) statement that '. . . rarity is merely the current status of an extant organism which, by any combination of biological or physical factors, is restricted either in numbers or area to a level that is demonstrably less than the majority of other organisms of comparable taxonomic entities.' In the rest of this chapter I consider how one might best go about deciding, on the basis of abundance and range size, precisely which species are rare.

1.2 CONTINUOUS AND DISCONTINUOUS MEASURES

Both abundance and range size are essentially continuous variables (although an abundance expressed as numbers of individuals can, of course, only have integer values). Moreover, for any natural assemblage it is unusual to find that species separate into discrete groups with abundances or range sizes of distinctly different magnitudes. Typically, an assemblage will comprise species with a range of different abundances and levels of spatial occurrence (for some exceptions see Chapter 2). Against this background it makes some sense to regard rarity as a continuous variable. That is, all species in essence are treated as rare, but some (those with low abundances or small ranges) are rarer than others (those with high abundances or large ranges). Thus, rarity would effectively be the inverse of the magnitude of abundance, of range size, or of some combination of the two.

It is difficult to find any compelling objections to regarding rarity as a continuous variable. Indeed, the term 'rare' is frequently used as a synonym for low abundance or small range, and as the converse of common or widespread, without any attempt to place hard limits on where rarity ends and commonness begins. Thus, Brown (1984) uses 'rare' to mean an extremely low density ('restricted' or 'local' was used to describe an extremely small spatial distribution), and Schoener (1987) uses it to mean occurrence in relatively few censuses and/or at relatively low abundances.

The chief arguments against regarding rarity as a continuous variable are twofold. First, that it essentially equates the study of rarity with the study of the whole of population biology, and de-emphasizes any claim rare species may have to be of special interest. Second, because for legal and conservation purposes species often need to be categorized as rare or otherwise, a more pragmatic approach is often desirable. As a consequence, many workers have chosen to treat rarity as a discontinuous or categorical variable.

This approach involves determining cut-off points for abundances and range sizes, below which species are regarded as rare. The position of such cut-off points will inevitably be rather arbitrary. They could be absolute values of abundance or range size, but this would give only very limited scope for comparative studies. If we want a general definition of rarity, cut-offs will have to be relative.

There are several ways in which relative cut-offs can be applied. I will consider three.

- Proportion of species: rare species are defined as the x% with the lowest abundances or smallest range sizes in the assemblage.
- Proportion of sum: rare species are defined as those with abundances less than x% of the summed abundances of all species in the assemblage, or as those with a range size less than x% of the largest range size possible in the study area.
- Proportion of maximum: rare species are defined as those with abundances or range sizes less than x% of those of the species that have the highest abundance and the largest range size in the assemblage.

The application of these methods to a data set is illustrated in Table 1.2. The most appropriate value of x may vary for the different methods and need not

Table 1.2 Examples of the delineation of rare species (bracketed) using proportion of species (Spp), proportion of sum (Sum) and proportion of maximum (Max) definitions, with cut-off points of (a) 25%, and (b) 5%. Data are the mean numbers of dung beetles of different species caught per trap in the spring at a site in the Mediterranean, from Lumaret and Kirk (1991)

	Species	*Abundance*	*Spp*	*Sum*	*Max*
(a)	1	1			
	2	1			
	3	1			
	4	2			
	5	3			
	6	5			
	7	5			
	8	7			
	9	10			
	10	13			
	11	18			
	12	21			
	13	28			
	14	31			
	15	49			
	16	67			
	17	97			
	18	107			
	19	130			
	20	1685			
	Total	2281			
(b)	1	1			
	2	1			
	3	1			
	4	2			
	5	3			
	6	5			
	7	5			
	8	7			
	9	10			
	10	13			
	11	18			
	12	21			
	13	28			
	14	31			
	15	49			
	16	67			
	17	97			
	18	107			
	19	130			
	20	1685			
	Total	2281			

be the same for abundances and range sizes. If the definition of rarity is to be general, the same values would, however, have to be used with all assemblages.

These different methods of applying cut-offs have varying strengths and weaknesses. A proportion of species methods results, by definition, in at least some species in any assemblage being labelled as rare (unless the assemblage is sufficiently species poor that x% is a fraction of a species). Using either of the other methods the proportion of species that are defined as rare would depend entirely on the shapes of the frequency distributions of species' abundances and range sizes. Since neither of these are constants but may take radically different forms (Chapter 2), these proportions may vary markedly. It is quite possible with these methods that there may be assemblages for which no species fall into the rare category. Using the proportion of sum method, it is also possible that assemblages would exist in which all species would be classified as rare. In terms of the proportions of species that are categorized as rare the proportion of species method would seem the most appropriate, as it is generally accepted that assemblages typically contain some rare and some common species. It also has the probably desirable property that the number of rare species in an assemblage is a direct function of species' richness. The more speciose the assemblage, the more species will be classified as rare. How numbers of rare species relate to the richness of an assemblage using either the proportion of sum or the proportion of maximum definition is less obvious. Though they would tend to increase with increasing richness in both cases, the function by which they do so may be case specific.

A further advantage of the proportion of species definition, as against either the proportion of sum or the proportion of maximum, is that it requires less information to delineate rare species. A simple ranking of species' abundances or range sizes, or recognition of the x% of species with the smallest abundances and range sizes is sufficient. If the proportion of sum definition is to be based upon abundances it is necessary to be able to estimate the actual abundances of all the species in the assemblage to calculate their summed abundance. If the proportion of maximum definition is to be applied it is necessary to estimate the abundance or range size, respectively, of the most abundant or widespread species, to rank the other species on the appropriate variable, and to determine the abundances or range sizes of the other species in the vicinity of the cut-off point sufficiently accurately so that this point can reliably be defined.

All three of the definitions suffer from the same potential drawback because they are based on relative rather than absolute criteria. That is that, through time, a particular species may move in and out of the rare category even though it maintains a stable abundance and spatial distribution and the composition of the assemblage remains constant. This may happen because changes in the abundances or range sizes of the other species determine whether or not it falls above or below the chosen cut-off point.

Tables 1.3 and 1.4 are collations of the criteria by which rare species have been delineated in a number of studies (many additional authors provide no

Table 1.3 The criteria by which a number of studies have delineated rare species on the basis of abundance and/or range size. The objectives of the different studies were varied (including avoidance of statistical biases and determining the amount of editing of distributional data required before producing maps). Definitions of classes of lower abundance or distribution than rare, if any, are given in square brackets

Source	*Taxon*	*Criteria*
Beebe (1925)	Various	Observed but seldom. [Unique, recorded but once from the research area. Probable, present in numbers just outside the research area]
Dony (1953, 1967)	Plants	Frequencies were calculated by visual impression
Bowen (1968)	Plants	Less than a thousand plants in any locality
O'Neill and Pearson (1974)	Birds	Seen regularly but in small quantities. [Isolated, seen irregularly. Accidental, recorded not more than twice]
Perring and Walters (1962)	Plants	Recorded from ≤20 vice-counties (<14% of total)
Ridgely (1976)	Birds	Recorded on fewer (usually considerably fewer) than 25 % of trips in proper habitat and season (a 'trip' is considered to be a day's field work) [Very rare, records extremely few anywhere in Panama, and always in small numbers, but presumed to be a resident within the country, or within the expected range of a migrant or wanderer]
McGowan and Walker (1979)	Copepods	$<10^2$ individuals in the 62 samples analysed. [Very rare, <10 individuals]
Ridgely and Gaulin (1980)	Birds	Recorded only occasionally
Roberson (1980)	Birds	Has occurred, during the most recent 5 year period, an average of four times or less in any West Coast state or province
Werner (1982)	Anurans	Seen (or heard) less than 25% of the time (less than one sighting for every four trips)[a]
Hartshorn and Poveda (1983)	Trees	0.1–0.01 mature individuals/ha. [Very rare, <0.01/ha]
Stiles (1983)	Birds	Seen regularly at longer intervals [than Uncommon, defined as one or a few seen at frequent intervals, usually not daily] in small numbers. [Occasional, seen sporadically; usually at longer intervals, in small numbers (but also applies to occasional flush 'invasions'). Accidental, five or fewer records to date]
DeSante and Pyle (1986)	Birds	Generally not expected on any given day. Typically no more than a few are detected on fewer than 10 % of the days. The actual number of occurrences for a state or province in any given season can vary from as few as 11 recent records to as many as 30 records/year. [Extremely rare, ten or fewer records for the past 50 years for the state or province in the given season]

Table 1.3 continued

Source	*Taxon*	*Criteria*
Jefferson and Usher (1986)	Plants	Occurring in 50 or fewer 10 km squares in the British Isles
Bushnell *et al.* (1987)	Invertebrates	One organism collected during a field season
Youtie (1987)	Insects	Fewer than 10 individuals collected
Goodman *et al.* (1989)	Birds	1–100 individuals ('abundance designations are generally based on the authors' subjective estimate of the maximum number present in the country on any given day. This includes the number of passage and winter visitors, and for residents the number of breeding pairs')
Tonn *et al.* (1990)	Fish	Occurring in five or fewer lakes, out of possible totals of 113 and 51
Verkaar (1990)	Plants	Occurring in <30 25 km^2 grid squares, out of a total of 1677 in the Netherlands
Basset and Kitching (1991)	Arthropods	One individual collected
Buzas and Culver (1991)	Foraminifera	Recorded from 1 or 2 localities in a geographic area
Landolt (1991)	Plants	Up to 200 individuals or very local [very rare, up to 20 individuals]
Laurance (1991)	Mammals	<1% of all captures
Morgan *et al.* (1991)	Birds	Average relative abundance of 0.01–1.00
Avise (1992)	Various	$<10^4$ individuals

[a] Criterion suggested, but not applied to any data.

indication of the criteria by which species were designated as belonging to different categories). In virtually all instances these criteria are based on measures of species abundances or levels of spatial occurrence. Almost none of the studies state the rationales by which cut-off points were arrived at. Moreover, although rare species may, for example, have been defined as those having abundances that are less than x% of the summed abundances of all the species in an assemblage or of the largest possible range, one cannot usually tell whether this value was chosen because it is a definition the authors usually apply or because the number of rare species it generates seems to be about right! One suspects that it is often the latter. That is, what appear to be proportion of sum criteria are used to apply a proportion of species definition of rarity. Clearly, the net result of the variety of methods is that the proportion of species eventually treated as rare in a study varies enormously (Table 1.4).

Table 1.4 The criteria by which a number of studies have been delineated as rare species, and the proportion of the total number of species in the assemblage (N) which these comprise (% Spp.). In all cases the numbers refer to the spatial scale at which rarity was defined. The objectives of the different studies were varied

Source	*Taxon*	*N*	*Criteria*	*% Spp.*
Hall and Moreau (1962)	Birds			
	Ethiopian	1700	Range does not extend more than 250 miles in any direction	5.6
	Palaearctic	1100		<1.8
	Nearctic	750		1.2
	Australia	520		2.3
Munves (1975)	Birds	81	Seen only a few times	9.9
Karr (1977)	Birds			
	Panamanian site	172	Seen only once or, at most, a few times during the study	44.8
	Costa Rican site	331		24.8
Pearson (1977)	Birds		<0.04 sightings per hour of observation	
	Sites in:			
	Ecuador	254 (95)[a]		79.5
	Peru	214 (83)		81.8
	Bolivia	207 (83)		76.8
	Borneo	142 (34)		59.9
	New Guinea	114 (31)		49.7
	Gabon	154 (42)		72.7
Thomas (1979)	Birds	243	Found less than five times	14.8
Haila and Järvinen (1983)	Birds	121	Observed at most five times in line transect counts	37.2
Pickard (1983)	Angiosperms	180	Common and very uncommon species occurring on <10% of 437 m grid squares and abundant species on <5% of squares	27.8
	Ferns	43		27.9
Maitland (1985)	Fish	54	Native species with only a few known populations in the British Isles, or native species the populations of which are potentially unique individually and decreasing in number	14.8[b]
Goeden and Ricker (1986)	Insects on			
	Cirsium californicum	58	Collected at one or two sites from a possible 28	50.0
	Cirsium proteanum	31	Collected at one or two sites from a possible 12	71.0
Hubbell and Foster (1986)	Plants	303	Average density <1 individual/ha	36.6
Usher (1986a)	Plants	65	Not more than 10 individuals or three clumps in the field	26.2

Table 1.4 continued

Source	*Taxon*	*N*	*Criteria*	*% Spp.*
Roubik and Ackerman (1987)	Orchid-bees			
	Site SR	46	log. of mean annual abundance <0.6	23.9
	Site PR	43		27.9
	Site CC	50		26.0
C. Nilsson *et al.* (1988)	Plants	366	Recorded from one to two sites out of a possible 149[c]	23.5
Adsersen (1989)	Plants	604[d]	Rarely collected, or occur only in areas where human exogenous impacts threaten the vegetation structure or the species itself	23.8[d]
Deshaye and Morisset (1989)	Plants	271	Occurred in 1–5 island-habitats (sum of the numbers of habitats on every island in which this species was present) out of a possible 248	31.4
Dzwonko and Loster (1989)	Plants	114	Occurred in ≤1/10 of localities	49.1
Faith and Norris (1989)	Macro-invertebrates	269	Have abundances comprising ≤0.5% of total abundance of all taxa	92.6
Rands and Myers (1990)	Amphibians	52	Rarely seen[e]	13.5
	Reptiles	82	Rarely seen	18.3
Longton (1992)	Mosses	692	Recorded in 15 or fewer 10 km squares of the British national grid since 1950 during an extensive field survey	25.6[f]
Osborne and Tigar (1992a)	Birds	285	1–100 individuals	49.5

[a] Figures in parentheses are the number of unseen but potentially occurring species included in the rare class.
[b] 19% using total for native species only (12 are introduced).
[c] In this instance the stated criterion was actually the proportion of species desired to be classified as rare, and the numbers of sites was the cut-off point to achieve this.
[d] Species + subspecies.
[e] Includes species which are possibly extinct.
[f] Includes about 15 species that appear to be extinct in Britain.

1.3 SCALE DEPENDENCE AND INDEPENDENCE

Whatever definition of rarity one uses, the results it gives will be influenced by the spatial scale at which it is applied. The studies in Tables 1.3 and 1.4 define rarity at a variety of spatial scales. Thus, Hall and Moreau (1962) define it at the level of entire biogeographic regions, and Karr (1977) defines it on the basis of occurrences on his study plots. While some would clearly prefer to reserve the term 'rare' for use only with respect to species' global populations and entire geographic ranges most would accept that there will be some species, albeit different ones in each case, that can be regarded as rare at any given spatial scale (e.g. Harper, 1981). A consequence of the latter position is that a species may be rare on one scale but not on another. Pigott (1981), for example, argues that while *Tilia platyphyllos* might be regarded as the rarest native species of tree in northern Europe, it is widely distributed in Europe as a whole and would not be regarded as rare on this scale (Figure 1.1).

While it is generally accepted that 'abundance' may be determined at virtually any spatial scale, it is something of a departure from what is accepted as normal usage to use 'range' equally broadly (although a few authors have applied the term at several scales). In particular, 'range' is not often applied to spatial occurrence at a local scale. To do so, does, however, have the great advantage of minimizing confusion between the various meanings of the alternative word 'distribution'. Because much of this book will be concerned both with the spatial 'distribution' of individuals and with the form of frequency 'distributions', I have chosen to avoid this potential confusion as

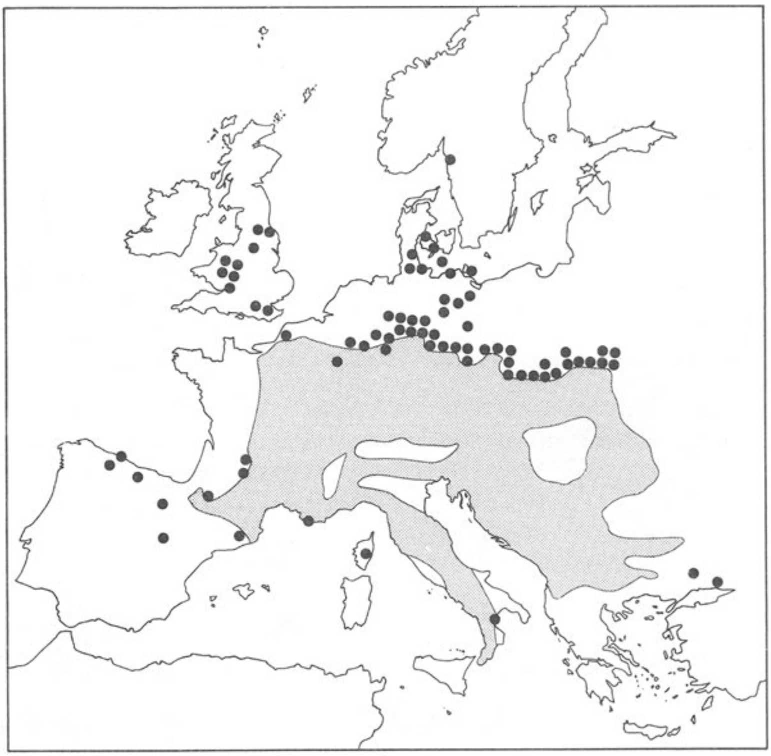

Figure 1.1 Occurrence of the tree *Tilia platyphyllos* in Europe. (Redrawn from Pigott, 1981.)

much as possible by regarding 'range' as a generic term covering all spatial scales. For greater precision, where necessary, three different prefixes will be used. 'Micro-range' will be used to mean a distribution at a local scale (a small area of homogenous habitat), 'meso-range' to mean a distribution at a regional scale (an area large enough to embrace many habitats, but not so large as to encompass the entire geographic ranges of a significant proportion of the species in an assemblage), and 'macro-range' will be used interchangeably with 'geographic range' to mean a distribution at a biogeographic scale (an area large enough to encompass the entire geographic ranges of the majority of the species in an assemblage). Of these, the area over which meso-ranges are measured is perhaps the most liable to be arbitrary. Typical limits might be those of a large true island, which would be reasonably natural, or the boundaries of a mainland state or country, which frequently would not be so.

The particular spatial scale at which a study is performed may not only determine which species are regarded as rare. It may also have profound effects on which processes have given rise to that rarity and to any patterns that are observed in it. This will be a repeated theme of later deliberations (especially in Chapters 4 and 6).

Although the categorization of species as rare or otherwise (or, using a continuous definition, as rare and less rare) is made with respect to one particular spatial scale, this does not mean that this is the only scale at which this categorization may be of interest. One might, for example, determine which species are and which are not rare on the basis of their global abundances or range sizes, and then explore how the numbers of these rare species that are present differ between regional or local assemblages of varying sizes or of the same sizes in different places. Thus, White *et al.* (1984) examined how the numbers of rare species, defined on the basis of their restricted range at state and national levels, changed between much smaller areas that differed in their overall species richness.

The recognition that rarity can be defined at different spatial scales has some important consequences. Foremost, it suggests a way out of the apparent contradictions in widespread beliefs that, for example, tropical organisms tend to be rare, and that within the tropics some species are common. Both statements can be true, dependent upon the scales at which rarity is determined. Tropical organisms may tend to be rare at a global scale, while at the scale of the tropics many will not be regarded as such.

Of course, although the concept of rarity can be applied at almost any spatial scale, it is of primary interest and has been most extensively studied at regional or biogeographic levels. Discussion of rarity in this book will reflect that emphasis.

1.4 ENDEMISM AND RARITY

At large scales, the concept of rarity is closely allied to that of endemism. Species are endemic to an area if they occur within it and nowhere else. They will thus tend to have smaller range sizes and abundances than those species which are not endemic. Endemism and rarity are not, however, interchangeable. Species may be endemic to an area and yet occur throughout it at levels of abundance or occurrence greater than those of many, or even most, of the other species found there. Likewise, at the level of some islands, virtually all the species are endemic, yet it would be of little value to regard them all as rare at this scale. Kruckeberg and Rabinowitz (1985) state, 'The narrow or local endemic is the one that best fits the colloquial notion of rarity. However, the term endemism, in its classical biogeographic usage does not necessarily imply rarity or even small range'.

1.5 DELINEATING AN ASSEMBLAGE

Just as the concept of rarity can be applied at different spatial scales, it can also be applied to assemblages the bounds of which are constrained in different ways.

1.5.1 Taxonomic constraints

Perhaps the most obvious limits that can be manipulated are taxonomic. Increasing or decreasing the numbers of taxa which are included as members of an assemblage will change which species are categorized as rare. There may be two reasons. First, even though the methodology used remains constant, the numbers of species so defined are liable to change. Second, while most taxa have species which have very few individuals and very small range sizes, they may vary drastically in the maximal abundances and range sizes which species attain.

Again, as with spatial scales, species can be categorized as rare with reference to a broad assemblage, and then the classifications used to address questions about the distribution of rare species among their component taxa. Hall and Moreau (1962) find that, by their definition, 5.6% of birds in the Ethiopian region are rare (Table 1.4), but that these comprise 8% of the passerines, and within the passerines 6% of the Estrildidae, 5% of the Muscicapinae, 12% of the Nectariniidae, 11% of the Ploceidae, 13% of the Sylviinae and 14% of the Turdinae.

1.5.2 Vagrancy

Regardless of the taxonomic limits placed on an assemblage, not all of the species which it contains have equal status. In particular, at local and regional scales, many are not permanent members of the assemblage, do not breed, or do not have self-sustaining populations in the area of interest. Such species have been variously termed accidentals, casuals, immigrants, incidentals, strays, tourists, transients and vagrants; I shall refer to them as vagrants. Typically, though not necessarily, they occur at low abundances and have small

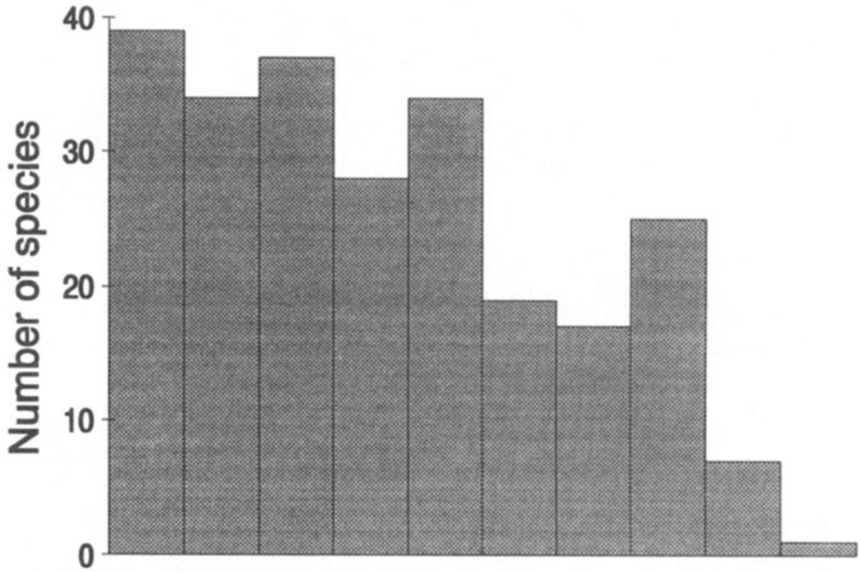

Figure 1.2 Frequency distribution of the numbers of accepted records of rare bird species in Britain in the period 1958–1989. Abundance classes are 1 individual, 2–3, 4–7, 8–15 etc. (From data in Whiteman and Millington, 1991.)

range sizes in a study area. If included in classifications, they stand a disproportionately high probability of being categorized as rare. The vast majority of the bird species regarded as rare in Britain are vagrants and have very low abundances (Figure 1.2).

The criteria by which vagrants are recognized are varied and, as in delineating species which are rare, cut-off points are ultimately arbitrary. Notwithstanding, they are generally regarded as constituting an often high proportion of species richness. Thus, Hubbell and Foster (1986) regard many of the rare species of trees occurring on their 50 ha study plot of old-growth forest on Barro Colorado island as immigrants established from second-growth forest. Osborne and Tigar (1992a) record large numbers of the less abundant birds of Lesotho as non-resident (Table 1.5), with among the probable non-breeding visitors 49 species visiting the country regularly and a further 51 only occasionally. Pimentel and Wheeler (1973) class almost half of the arthropods encountered in their study of alfalfa as incidental to the system (Table 1.6).

Shmida and Wilson (1985) argue that mass effects, the flow of individuals of species into areas where they cannot maintain viable populations (i.e. vagrants), are one of four biological determinants of species richness (the others being niche relations, habitat diversity and ecological equivalency). Following many others, Stevens (1989) proposes that mass effects are

Table 1.5 Numbers of species of different status in the lower abundance categories of the birds of Lesotho. Figures are for confirmed and suspected breeding, those in parentheses for confirmed breeding only. Very rare, 1–10 individuals; rare, 10–100; scarce, 100–1000; and special, species which although not scarce in Lesotho are of regional or international importance. (From Osborne and Tigar, 1992a.)

	Resident	*Non-resident*	
	Breeding	*Breeding*	*Non-breeding*
Very rare	12 (5)	5 (2)	73
Rare	27 (7)	2 (0)	22
Scarce	25 (18)	5 (5)	5
Special	5 (5)	1 (1)	0
Totals	69 (35)	13 (8)	100

especially important in generating the high levels of local richness observed in much of the tropics.

How vagrants are best treated in the context of rarity will very much depend upon the questions that are being asked. From a conservation perspective they should usually be ignored, on the grounds that because they cannot maintain viable populations they are not suitable candidates for management, or at least there are almost certainly areas where management would be far more effective. From an ecological perspective, however, vagrants may perhaps best be regarded as part of the assemblage because they contribute to a potentially large number of between-species' interactions.

Table 1.6 Number of arthropod species of different status in an alfalfa community. Herbivores: primary, development completed on alfalfa; secondary, some nourishment derived from alfalfa; incidental, no feeding observed to occur on alfalfa. Predators (and Parasites): primary, development completed while feeding on prey in the alfalfa community; secondary, any of its states observed to take prey from alfalfa; incidental, no prey was observed taken from alfalfa. (From Pimentel and Wheeler, 1973.)

	Number of spp.		*Number of spp.*	*(%)*
Primary herbivore	46	All primary	138	(23.4)
Secondary herbivore	145	All secondary	196	(33.2)
Incidental herbivore	121	All incidental	257	(43.5)
Primary predator	46			
Secondary predator	51	Total	591	
Incidental predator	119			
Primary parasite	46			
Incidental parasite	17			
Total	591			

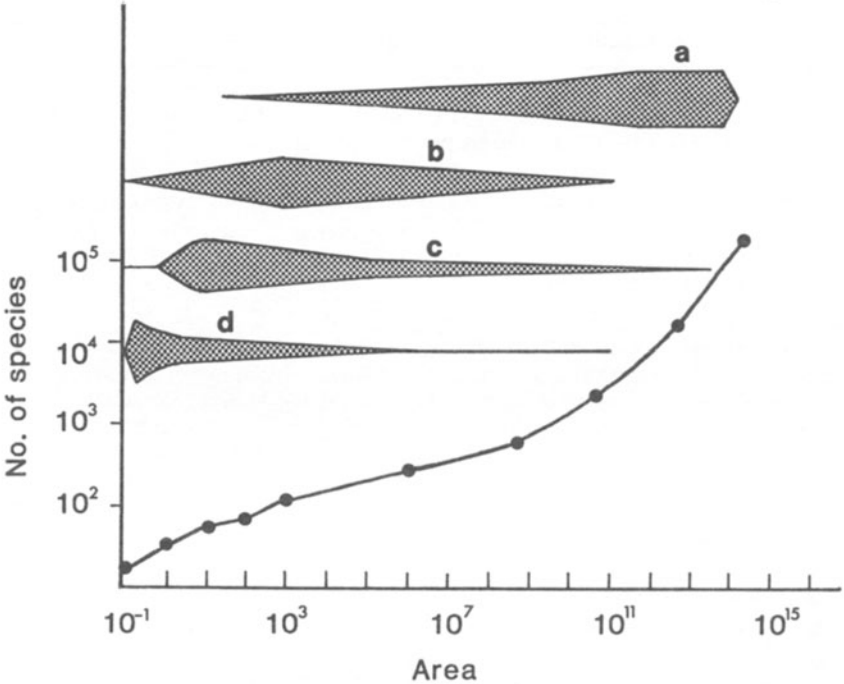

Figure 1.3 Nested species–area relationship for plants, spanning samples in the mattoral in Israel to the entire world (area measure in m^2). The hatched areas represent the hypothesized relative contribution of biological determinants to species' richness at different spatial scales; a, ecological equivalency; b, mass effect; c, habitat diversity; and d, niche relations. (Redrawn from Shmida and Wilson, 1985.)

The magnitude of the complications which vagrants generate may be scale dependent. Shmida and Wilson (1985) propose that mass effects are most important at meso-scales (Figure 1.3). Their effects will decline at scales which exceed the majority of dispersal distances of species, while at very small scales the numbers of vagrants are limited by the size of the target area. Nonetheless, vagrants are almost invariably present at any scale less than the global.

1.6 RARITY AND VULNERABILITY

Thus far, I have not mentioned what is perhaps the most widespread formal use of the term 'rare' in biology. That is, in schemes of classification which have been developed to categorize species on the basis of their supposed risk of extinction. There are many of these schemes. Perhaps the best known is that presently used by the International Union for Conservation of Nature and Natural Resources (IUCN), in which species are variously categorized as extinct, endangered, vulnerable, rare, indeterminate, out of danger, or insufficiently known (Table 1.7). This categorization, and its variants, forms the basis

Table 1.7 Definitions of the IUCN Red Data categories. (From Davis *et al.*, 1986.)

Extinct (Ex) Taxa which are no longer known to exist in the wild after repeated searches of their type localities and other known or likely places.
Endangered (E) Taxa in danger of extinction and whose survival is unlikely if the causal factors continue operating. Included are taxa, whose numbers have been reduced to a critical level or whose habitats have been so drastically reduced that they are deemed to be in immediate danger of extinction.
Vulnerable (V) Taxa believed likely to move into the Endangered category in the near future if the causal factors continue operating. Included are taxa of which most or all of the populations are decreasing because of over-exploitation, extensive destruction of habitat or other environmental disturbance; taxa with populations that have been seriously depleted and whose ultimate security has not yet been assured; and taxa with populations which are still abundant but are under threat from serious adverse factors throughout their range.
Rare (R) Taxa with small world populations that are not at present Endangered or Vulnerable, but are at risk. These taxa are usually localized within restricted geographical areas or habitats or are thinly scattered over a more extensive range.
Indeterminate (I) Taxa known to be Extinct, Endangered, Vulnerable or Rare but where there is not enough information to say which of the four categories is appropriate.
Out of Danger (O) Taxa formerly included in one of the above categories, but which are now considered relatively secure because effective conservation measures have been taken or the previous threat to their survival has been removed. In practice, Endangered and Vulnerable categories may include, temporarily, taxa whose populations are beginning to recover as a result of remedial action, but whose recovery is insufficient to justify their transfer to another category.
Insufficiently Known (K) Taxa that are suspected but not definitely known to belong to any of the above categories, because of lack of information.

of the *Red Data Books* (e.g. Williams and Given, 1981; Perring and Farrell, 1983; see P. Scott *et al.*, 1987 for a historical review). Such lists may serve several functions, for example: as a resource document for conservation (e.g. planning reserves, controlling or modifying development, formulating management plans); providing a focus for the centralized input of new information; as a useful information source for publicizing the plight of endangered species; for legislative purposes; and as a focus for planning research (McIntyre, 1992).

Munton (1987) provides an excellent review of the methods by which species have been categorized as under different degrees of threat. In the course of this review, he placed a selection of the categories that have been used into different classes. By and large, those schemes which included a rare category

Table 1.8 A selection of 57 categories from schemes classifying species on the basis of threat, placed in various classes. Categories in brackets occur in more than one class. (From Munton, 1987.)

Species has disappeared
Extinct, Probably extinct, Extirpated recently, Extirpated, Known only from osseous remains, Species presumed extinct, Practical extermination, Absolute extermination, Extermination in wild state

Species is under threat
Threatened, Threatened phenomenon, Commercially threatened, Community endangered through trade, Almost extinct, Species is likely to become endangered, Very gravely threatened, Potentially threatened, Threatened with early extermination, Species in great danger, Threatened with extinction

Species is declining
Declining species, Endemic and slowly decreasing, Depleted, (Very rare and decreasing)

Species is found only in small numbers
Rare, Very rare and decreasing, Extremely rare, Very rare but believed to be stable or increasing, Less rare but decreasing, Formerly rare but no longer in danger, Some rare birds probably not in immediate danger, Small populations, Less rare but believed to be threatened, Unique, The rarest, Exceptionally rare, Sufficiently rare

Species is only found in a small area
Peripheral, Disjunct, Limit of range relict, Endemic (Endemic and slowly decreasing), Restricted local

There is a lack of data on species status
Undetermined, Hypothetical, Insufficiently known, Status undetermined, Status inadequately known – survey required, data sought

Miscellaneous
Care demanding, Additional species, Out of danger, Neither rare nor threatened, Migratory

Monitoring needed
Situation à surveiller, Species need monitoring

of some description defined it as containing those species which were only found in small numbers (Table 1.8). Some more detailed examples are provided in Table 1.9. Munton states, however, that 'rare' is the most confusing of all the categories which are commonly used, because opinion is divided over the significance of the phenomenon. He also recognizes two problems associated with the 'rare' category. First, by ignoring differences in the spatial distribution of small populations it confounds species which may need to be protected in different ways (e.g. a species with a small population located at a single site and a species with a small population that is spread over a large region). Second, because by itself rarity does not indicate a species' risk of extinction (see Chapter 7) it would be more logical to use rarity as a parameter for the assignment of species to different categories of threat rather than as a category itself. Indeed, such an approach has essentially been taken in proposals to redefine the IUCN categories of threat (Mace and Lande, 1991).

Table 1.9 Examples of definitions of rarity from schemes classifying species according to how threatened they are. From the collation of Munton (1987), in which the full references can be found

- Ashton, R.E. (1976) Endangered and Threatened Amphibians and Reptiles of the United States
  Rare: Those species that are considered rare throughout the state or are found in environmental conditions disjunct from the normal geographic range of the species.
- Ayensu, E.S. and De Philipps, R.A. (1978) Endangered and Threatened Plants of the United States
  A *rare* species of plant is described as one that has a small population in its range. It may be found in a restricted geographic region or it may occur sparsely over a wide area.
- Frugis, S. and Schenk, H. (1981) Red List of Italian Birds
  Rare species: Species present in Italy with small populations which at present are not threatened nor considered vulnerable but whose 'natural' rarity puts them in peril.
  Status:
    Species which in Italy are on the edge of their geographical range.
    Species whose populations are very local within their range or which are present with very low density even on a wider range
    Species of recent (post 1950) establishment in Italy and whose populations need special conservation measures to facilitate their spreading into suitable habitats and their permanent establishment
- Given, D.R. (1981) Rare and Endangered Plants of New Zealand
  Rare (R): Only small populations are known or the species is found only in restricted areas where it may be locally common. For the most part however the numbers of plants and localities where it is found are reasonably stable.
- Heintzelman, D.S. (1971) Rare and Endangered Fish and Wildlife of New Jersey
  Rare: A rare species is not presently threatened with extinction, but it occurs in such small numbers in New Jersey that it may become endangered if its environment deteriorates further or other limiting factors change. Careful watch of its situation is essential.
- Miller, R.R. (1972) Threatened Freshwater Fishes of the US
  Rare: Not under immediate threat of extinction, but occurring in such small numbers and/or in such a restricted or specialized habitat that it could quickly disappear.
- Tanasiychuk, V.N. (1981) Data for the 'Red Book' of Insects of the USSR
  Rare species, not yet directly threatened with extinction, but occurring in small numbers or in such small areas they may rapidly disappear.

The variety of ways in which the 'rare' category has been constrained in the generation of lists of threatened species and in population and community biology more broadly, makes for complications in drawing parallels between the two sets of schemes. Nonetheless, some rough-and-ready rules can be suggested. In most instances, species which are listed as rare in terms of their risk of extinction, together with those species which are regarded as being under threat, will also be viewed as rare in strictly ecological studies when rarity is defined at the same spatial scale (although there will be exceptions). The converse is less likely to be true there are frequently many species which are regarded as rare in ecological categorization schemes, but do not enter lists of threatened species.

1.7 THE USE OF 'RARITY' IN THIS BOOK

Drawing together various considerations (e.g. ease of use, past usage, versatility), I favour a discontinuous definition of rarity based on a proportion of species' constraint. More particularly, I suggest that a useful cut-off point is the first quartile of the frequency distribution of species abundances or range sizes (i.e. a cut-off of 25%). From a practical perspective 25% is a convenient figure, as it is frequently possible to determine this group of species. With poor sampling, many species may be recorded as having low abundances or small range sizes of the same magnitude, thus it is more difficult to determine those species comprising smaller proportions. A cut-off of 25% is also not greatly at odds with many of the studies listed in Table 1.4. By way of shorthand, this will be referred to as the quartile definition.

Where convenient, the quartile definition has been applied throughout this book. It has proved a useful tool in formulating many of the ideas expressed. Its application has been rather more limited than one might have hoped, because it is often difficult to apply retrospectively to published studies. The same would, however, be true of virtually any other strict definition. Perhaps one of the greatest advances to the study of rarity would be the establishment of recognized criteria for its identification, or at least the analysis of data using such criteria in parallel with any other criteria thought by individual workers to be preferable. Those species defined as rare under the quartile definition are indicated in many of the figures used in subsequent chapters; they are delineated on abundance and range size on both axes, by dashed lines.

Some additional points about the use of rarity in this book should also be made. First, in the spirit of minimizing the prejudgment of the causes and consequences, rarity is defined in terms of abundance *or* range size. The interactions between the two classifications, which result for the same assemblage, are explored at some length (Chapter 3). The temptation to regard species falling in or out of the first quartiles of the frequency distributions of species' abundances and/or range sizes as forming different kinds of rarity or non-rarity has been resisted. There have been many attempts to recognize, and sometimes label, different forms of rarity (Griggs, 1940; Good, 1948; Mayr, 1963; Drury, 1974; Stebbins, 1978a; Terborgh and Winter, 1980; Rabinowitz, 1981a; Main, 1984; Cody, 1986; Soulé, 1986; Rabinowitz *et al.*, 1986; Arita *et al.*, 1990; Bawa and Ashton, 1991; McIntyre, 1992). Of these, the most well-known is that of Rabinowitz (1981a; Rabinowitz *et al.*, 1986) who categorized plant species according to geographic range (large or small), local population size (large or small) and habitat specificity (wide or narrow). Of the eight possible combinations of these states (Table 1.10) she recognized seven as constituting different forms of rarity (the eighth group (common species) have large populations and ranges, and wide specificities). In a similar

Table 1.10 The typology of rare species proposed by Rabinowitz (1981a). With the exception of the first which is listed, all combinations of the two states of each of the three characteristics are regarded as forms of rarity. Plant examples are given for various of the combinations (Rabinowitz, 1981a)

Geographic range	*Habitat specificity*	*Local population size*	
Large	Wide	Large, dominant somewhere	Locally abundant over a large range in several habitats (fat hen *Chenopodium album*)
Large	Wide	Small, non-dominant	Constantly sparse over a large range and in several habitats (knotroot bristle grass *Setaria geniculata*
Large	Narrow	Large, dominant somewhere	Locally abundant over a large range in a specific habitat (red mangrove *Rhizophora mangle*)
Large	Narrow	Small, non-dominant	Constantly sparse in a specific habitat but over a large range (*Taxus canadensis*)
Small	Wide	Large, dominant somewhere	Locally abundant in several habitats but restricted geographically (pygmy cypress *Cupressus pygmaea*)
Small	Wide	Small, non-dominant	Constantly sparse and geographically restricted in several habitats (Non-existent?)
Small	Narrow	Large, dominant somewhere	Locally abundant in a specific habitat but restricted geographically (*Shortia galacifolia*)
Small	Narrow	Small, non-dominant	Constantly sparse and geographically restricted in a specific habitat (*Torreya taxifolia*)

vein, Bawa and Ashton (1991) distinguish four kinds of rarity in tropical forest trees, species that are uniformly rare, species that are common in some places but rare in between, species that are local endemics, and species that are clumped even when overall population density is very low. In the main, such approaches have necessitated arbitrary, and often subjective, divisions to the breadth of values of yet more variables (e.g. habitat specificity, dispersal ability) in addition to abundance and/or range size. In this volume these additional variables will largely be treated as continuous and their interactions with abundance and range size will be explored.

Second, in using a definition of rarity that will identify different species as rare, dependent upon spatial scale and how an assemblage is delineated, rarity cannot be regarded as a species-specific characteristic. The only way in which this might be held to be true is at the global scale for a defined assemblage.

This minimizes conflict with the use of rarity with respect to levels of threat – species may be at a high risk of extinction at some spatial scales but not at others. Just how constant in composition the rare component of a defined assemblage is with respect to space and time is explored in Chapters 4 and 5, respectively.

Third, the terms 'common' and 'widespread' will be used as antitheses of rare, when rarity is defined in terms of abundance and range size, respectively. Their application avoids repeated reference to the not rare.