2 Species Richness

There are . . . more species of bird breeding, and also more wintering, in forests than in fields . . . more species of trees in eastern North America than in Europe, and more flies of the family Drosophilidae on Hawaii than anywhere else. There is an even more dramatic difference in the number of species in the tropics than in the temperate . . . Will the explanation of these facts degenerate into a tedious set of case histories, or is there some common pattern running through them all? [MacArthur 1972]

2.1 Introduction

An ecologist setting out to understand the workings of an animal assemblage or community will almost certainly begin by treading a well-worn path. No progress can be made until aspects of the community have been quantified, because without these data there is nothing to explain. A number of features can be measured, but among the questions first addressed will probably be how many species are present, what are their identities and characteristics, and in what numbers does each occur? These issues are fundamental because they define what occurs, and how much of it there is. In this chapter, we focus on the first of the questions, and examine the factors that are likely to determine the answer obtained.

Throughout, we will refer to the number of species in a defined area as the *species richness* of that area (following McIntosh 1967). We think this term is better than the commonly used alternative, *species diversity*, as that has typically been applied to the quantity measured by indices that take account not only of the number of species, but also of the distribution of individuals among them (see, for example, Hurlbert 1971; Magurran 1988). Thus, reference to species diversity hereafter can be taken as meaning a quantity assessed by such an index.

We address the question of how many species can co-exist in a given area before other questions, because the answers are particularly illustrative of the importance of the links between large- and small-scale patterns and processes. No pattern shows more clearly how an understanding of the structure of local assemblages requires a regional perspective. The bird fauna of Eastern Wood provides a prime example.

The avifauna we encountered in Eastern Wood can be viewed as the small-

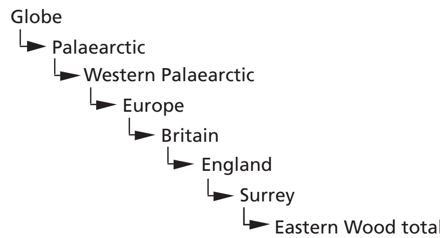

Fig. 2.1 The species richness of the avifauna of Eastern Wood constitutes a subsample of the avifauna from sequentially nested levels above.

est piece in a 'Russian doll-like' set of nested faunas, with the largest representing the global total number of bird species (Fig. 2.1). Each level down can be thought of as sampling a proportion of the fauna from the level above. What we wish to know is what causes each of these samples to assume the magnitude that it does.

2.1.1 *Species richness at the smallest scales*

The 25 species that we saw on our first visit to Eastern Wood represent almost 80% of the species shown by Beven (1976) typically to breed in the wood in any one year, and just over 50% of the total recorded as breeding in the period 1949–79. In other words, in just three hours in the wood we observed more than a half of the species recorded breeding over 30 years, a high proportion for so little effort. Nevertheless, and despite our best efforts, we failed to observe several species which one might have expected to find in the wood at that season. For example, mistle thrush, treecreeper and starling all eluded us. This failure could have arisen for several good reasons.

Some of those species missed will have been present in the wood at the same time as we were, and had our search continued we would ultimately have found them. This is a straightforward sampling effect, and lies at the heart of any attempt to determine the species richness of an area, be that area small or large. The more time spent, the more likely individual birds are to be encountered, and the greater the number of species that will be recorded. Typically, the rate of increase in the numbers of species observed is initially very high, and steadily declines (Fig. 2.2). In fact, over reasonably short periods of time or when reasonably few individuals are encountered, the pattern may be quite heterogeneous. Thus, on plotting the data for our own short visit to Eastern Wood (Fig. 1.2), we find that the rate of accumulation increased in the period immediately before our departure, suggesting that perhaps a longer stay would have been profitable!

The cumulative growth in numbers of species observed in an area with time constitutes a particular problem for the comparison of estimates of levels of species richness. While the cumulative number may approach an asymptote, it will never actually attain one. Species will forever continue to be added to the

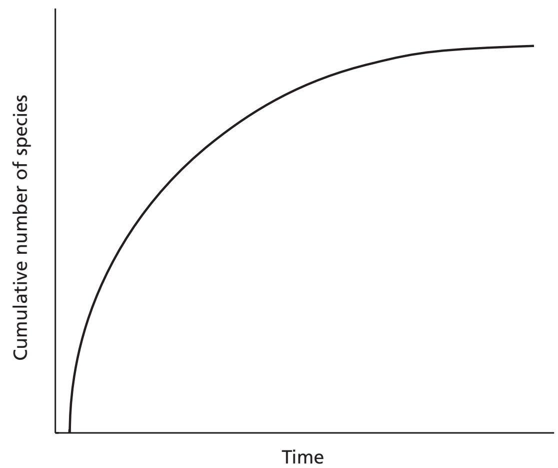

Fig. 2.2 Idealized species accumulation curve, showing the change in the rate at which new species are detected in an area by a given sampling protocol.

avifauna of any given area, albeit that the rate of addition ultimately will be extremely low. Based on this phenomenon, Grinnell (1922) estimated how long it would take before all the bird species recorded from North America had been seen in California. He wrote: '. . . it is only a matter of time theoretically until the list of California birds will be identical with that for North America as a whole. On the basis of the rate for the last 35 years, 1⅗ additions to the California list per year, this will happen in 410 years, namely in the year 2331, if the same intensity of observation now exercised can be maintained. If observers become still more numerous and alert, the time will be shortened.' (p. 375). It remains to be seen whether his prediction will be correct. However, at the present rate of discovery it is an overestimate of the time that will be needed (Bock 1987). In the period 1958–85, the number of bird species recorded in Britain grew at a rate of approximately 2–3 per annum (Fig. 2.3). If this rate continued, it would take about another 3500–4500 years to record all of the world's birds in the country!

The failure to record several of the species that one would have expected to see in Eastern Wood that April morning may not only be a consequence of simple sampling effects, but also of the probability of encountering species which are themselves moving in and out of the area. This is particularly problematical when sampling small areas, over relatively brief periods, for species with very large home ranges, such as many raptors. For example, sparrowhawks have bred erratically in Eastern Wood, a pair being present in some years and not in others (Appendix II). Yet, when they are not breeding there it is likely that the wood falls within the home range of sparrowhawks breeding at other sites (in any one year, Bookham Common as a whole could have held two to three pairs, and at least two further pairs occurred within 1 km of the common in the 1980s; Newton *et al*. 1997). This issue has been found to be par-

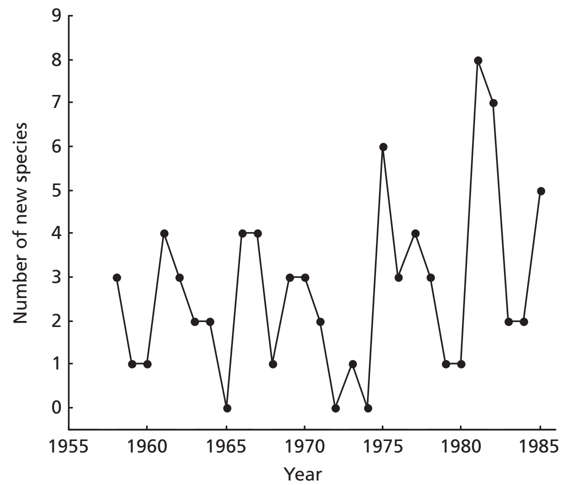

Fig. 2.3 The number of bird species previously unrecorded in the region added to the British list in each year in the period 1958–85. From data in Dymond *et al*. (1989).

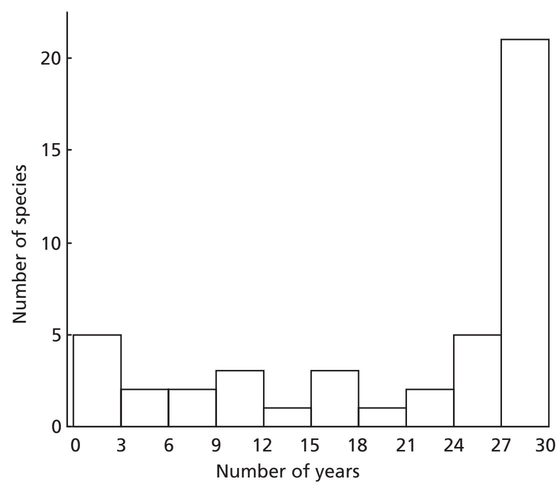

Fig. 2.4 Frequency distribution of the number of years in which individual bird species were recorded breeding in Eastern Wood in the period 1949–79. Recall that the maximum number of years is 30 because there was no census in 1957.

ticularly significant in evaluating the avian species richness of areas of moist tropical forest. Here, species may occur at very low densities and individuals may range over very large areas. Indeed, Terborgh *et al*. (1990) found that relative to the spatial requirements of their temperate zone counterparts, the territory sizes of Amazonian birds were roughly an order of magnitude larger.

Some of the species we would have expected to see in Eastern Wood may simply not have been present there in 1998. Not every species recorded in the wood breeds in every year. Indeed, the number recorded in any one year

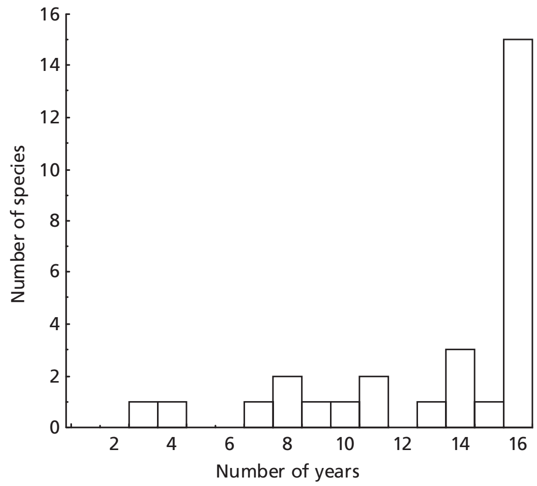

Fig. 2.5 Frequency distribution of the number of years in which individual bird species were recorded breeding in a 10-hectare plot of deciduous forest at Hubbard Brook, New Hampshire, in the period 1969–84; $n = 29$. From data in Holmes *et al.* (1986).

varied from 27 to 36 (Fig. 1.3). Figure 2.4 shows the frequency distribution of the number of years in which each bird species was recorded breeding in the period 1949–79. While most were recorded in most years, almost 50% of species were absent for at least three census years, and only one-third of species bred in every year of the 30. Similarly, the number of bird species breeding on a 10-hectare study area of temperate deciduous forest at Hubbard Brook in New Hampshire, USA, over a 16-year period, varied from 17 to 28, with a mean of 24 (Holmes *et al.* 1986). Of the cumulative total of 29 species, only 15 bred every year (Fig. 2.5). There are a variety of reasons for year-to-year variation in the species richness of an area, some of which we will encounter later. Nevertheless, species that one would expect to find at a site will inevitably be missed because of it.

The species recorded on our first visit comprise a significant fraction of the total breeding avifauna of Eastern Wood in the period 1949–79, which was 45 species. This is clearly an underestimate of the total fauna of the site, because the species richness of an area is affected by seasonality in the composition of the avifauna. Although we have no information on the number of bird species wintering in the 16 hectare of Eastern Wood, data are available for a 25-hectare area of oak wood lying within the boundaries of Northward Hill (High Halstow National Nature Reserve), Kent (Flegg & Bennett 1974). This is a comparable area of comparable habitat in a similar part of the country to Eastern Wood. Knowledge of the avian assemblage is based on censuses over a 12-year period (Flegg & Bennett 1974). The number of species recorded breeding at the site over this period was 43, of which 13 were present in the wood only in summer. This figure is probably quite close to the number of Eastern Wood breeders (Appendix II) that are only summer visitors, which on knowledge of general

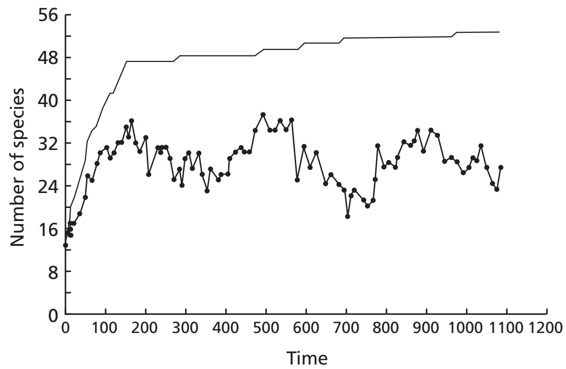

Fig. 2.6 The numbers (filled circles), and cumulative numbers (line), of species of bird recorded with time (days) over a 3-year period on censuses on transects through an upland forest on the Dandenong Ranges in Australia. Reprinted from Mac Nally (1997, with permission from Elsevier Science).

biology alone ought to be around 11 species. However, in addition to 30 resident species at Northward Hill, another 10 species were recorded in the wood only in winter. Thus, the wintering assemblage was only slightly smaller than the breeding one, but there was a significant degree of turnover between seasons. The same degree of turnover at Eastern Wood would add about a dozen extra species to the wood's bird list.

Mac Nally (1997) reports the results of a particularly impressive study of the effects of the temporal frequency of sampling on the sensitivity of monitoring of the avifauna of an upland forest in the Dandenong Ranges in Australia. Ninety-two separate censuses were conducted beginning in the winter of 1993 and continuing through to the end of autumn 1996. The number of species recorded varied markedly from one census to another, from as few as 12 to as many as 37, with this variation superimposed on an apparent pattern of seasonal variation in species numbers (Fig. 2.6). However, the cumulative number of species rose very rapidly, with 47 of the total of 52 species recorded being observed during just the first 17 censuses.

The degree of seasonal variation in the species composition of an area like Eastern Wood depends critically on the latitude at which that area lies. In western Europe, the proportion of species in local avifaunas in summer which are summer visitors increases with latitude, from 29% of breeding species at 35°N to 83% at 80°N (Newton & Dale 1996; see also Herrera 1978). Conversely, the proportion of winter visitors decreases with latitude from 36% of wintering species at 35°N to 8% of wintering species at 70°N and none at 80°N (Fig. 2.7). The overall number of species breeding or wintering tends to decline with increasing latitude (Section 2.5; with the primary exception of breeding coastal birds), as does the number of breeding or wintering species which are migrants (Fuller 1982; Cousins 1989; Newton & Dale 1996). Temporal decreases in the numbers of individual migrant birds in temperate areas,

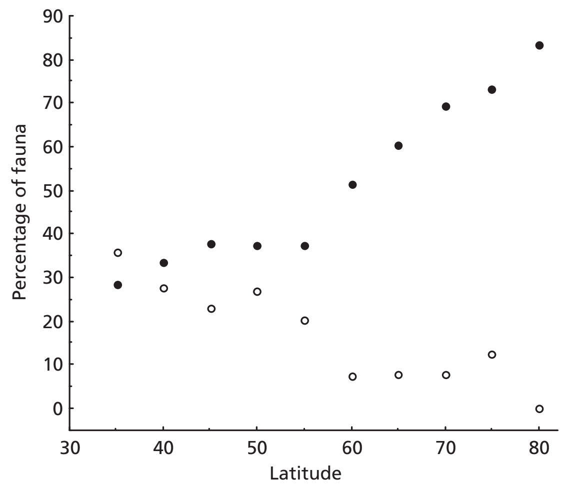

Fig. 2.7 Variation with latitude (degrees) in the percentage of species in an avifauna in Europe that migrate to other latitudes to winter (filled circles) and the percentage in the wintering avifauna that migrate to other latitudes to breed (open circles). From data in Newton and Dale (1996).

particularly neotropical migrants wintering in North America, are presently a cause of much concern (e.g. Leck *et al*. 1988; Robbins *et al*. 1989; Terborgh 1989; Hagan & Johnston 1992; James *et al*. 1996).

2.1.2 *Species richness at larger scales*

As will be continually stressed throughout this book, local sites are embedded in a regional context. Thus, the 45 species breeding in Eastern Wood in the period 1949–79 was about 37% of the 121 bird species that bred in Surrey, the county in which it sits, during the 20th century (data from Parr 1972). This number in turn constitutes just over half of the bird species recorded breeding in the whole of Britain in the 20th century, which at the date of our visit to Eastern Wood stood at 236 (data from Gibbons *et al*. 1996). Of these species, approximately 220 breed on a reasonably regular basis (Appendix III).

Good comparisons with the breeding avifaunas of other countries are difficult to provide, because few peoples have the same detailed knowledge of their avifaunas as do the British. Nevertheless, those comparisons that are possible reveal the British breeding avifauna to be relatively depauperate. One thousand and eleven landbird species alone have been recorded breeding in Colombia, and 835 in Ecuador, out of totals of 1093 and 906 landbird species, respectively (Rahbek 1997). Terborgh *et al*. (1990) carried out a census of a 97-hectare plot in a rainforest in Amazonian Peru over a 3-month period in 1982, and found 245 species holding territory or occupying all or part of the plot.

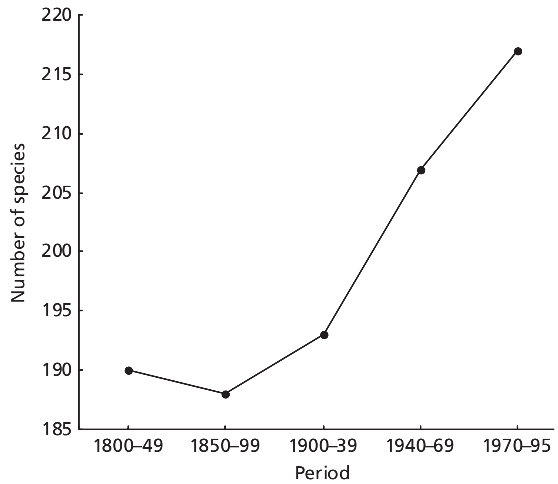

Fig. 2.8 The number of species of bird recorded breeding in Britain in different periods from 1800 to 1995. Note that later periods cover fewer years. From data in Gibbons *et al*. (1996).

Moreover, an additional 74 species visited the plot without breeding there. Thiollay (1994) recorded 248 bird species as regular visitors to a 100-hectare plot of rainforest in French Guiana over a 2-year period. The breeding species richness of local sites within Britain, and of Britain overall, pales in comparison with areas in the tropics.

Although the breeding avifauna of Britain is relatively poor, it is nonetheless higher than it was. Between about 1800 and the present, the total number of indigenous species breeding in Britain has increased by more than 25 (Fig. 2.8). The temporal turnover in the species present has, however, been more marked than this might imply. Over the whole period since 1800, 228 indigenous species have bred, compared with the 218 which did so in the period 1970–95 (Gibbons *et al*. 1996). Four which bred in the period 1800–49 did not breed in 1970–95 (long-tailed duck, Baillon's crake, great bustard, great auk), and 34 which bred in 1970–95 did not breed in 1800–49 (red-necked grebe, slavonian grebe, black-necked grebe, little bittern, whooper swan, gadwall, pintail, common scoter, goldeneye, goosander, common crane, black-winged stilt, little ringed plover, Temminck's stint, purple sandpiper, wood sandpiper, spotted sandpiper, Mediterranean gull, little gull, collared dove, snowy owl, shore lark, bluethroat, black redstart, fieldfare, redwing, Cetti's warbler, icterine warbler, firecrest, brambling, serin, parrot crossbill, common rosefinch, Lapland bunting). Over a similar period, 1850–70, Järvinen and Ulfstrand (1980) showed that Denmark, Norway, Sweden and Finland were colonized by an average of 2.8 bird species and lost 0.6 species per decade and country.

Burton (1995) attributes the pattern of species colonizations in Europe observed over the past 150 years to climate change. He notes that the period from 1850 to 1950 marked a warm phase, but that deterioration in the climate has occurred in the years since. He suggests that the warm period coincided with the northward and westward spread of several species of previously largely southern European distribution, such as the black redstart and serin, while the subsequent cooling prompted colonization by northern species such as the wood sandpiper, snowy owl and redwing. These northern species probably were not recorded breeding in Britain in the 50 years prior to the warm period of 1850–1950 because their small populations were overlooked by the equally small population of birders. Certainly, these species would have bred in Britain in prehistoric times, because the changes in the British avifauna observed over the last 150 years are but a small snapshot of the continual ebb and flow of species across the global landscape in response to climatic changes acting at larger spatial and temporal scales.

Over the last 400 000 years or so, Britain has probably been subjected to four periods of glaciation, separated by short interglacial periods such as that believed to be represented by the current climate (Petit *et al*. 1999). The advance and retreat of ice sheets across Europe inevitably caused major shifts in species distributions. There is good evidence from faunal remains that tundra was the predominant habitat in Britain at the height of some of the glaciations. Arctic bird species would inevitably also have been present. The climate in interglacial periods showed considerable variation. For some periods, temperatures were slightly higher than at present, suggesting that birds currently typical of southern Europe may have been widespread across Britain. At other times, the fauna apparently resembled that of present-day southern Scandinavia. Remains of elements of the avifauna deposited since the last glaciation certainly clearly indicate faunas associated with climates somewhat different to that experienced in Britain today. In particular, bones of both adult and fledgling Dalmatian pelicans identified in Iron Age Somerset reveal a flourishing British colony of a species now confined largely to the eastern Mediterranean. Climatic deterioration may have caused the extinction of this species in Britain, and would inevitably have contributed to many other changes in the avifauna (Burton 1995). Nevertheless, even in the warmest interglacial period, the British avifauna would not even remotely have approached the richness of that seen today in the moist tropics. Neither is it likely to do so in the foreseeable future, despite probable major changes in the composition of Britain's birds as a result of global climate change (Moss 1998).

The wintering avifauna of Britain is no more impressive than that breeding. In January 1991, one of us recorded 138 species of bird during a leisurely day with binoculars and a bicycle at Keoladeo National Park, Bharatpur, India. To produce a list of equivalent length in England on the same (or any) date over the same length of time would have involved equipment and planning worthy of a military operation. The typical entire wintering avifauna of Britain contains only slightly more species than this (Appendix III).

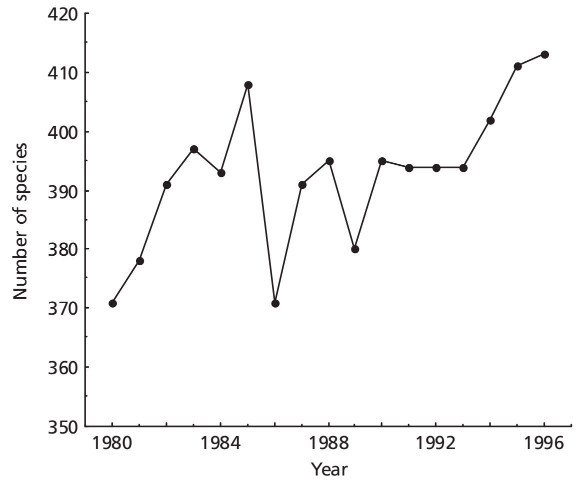

Fig. 2.9 The number of species of bird recorded occurring in the UK in each year in the period 1980–96. From data in Whiteman and Millington (1991) and http://www.uk400.demon.co.uk/yearlist.htm.

Britain may fare poorly in comparison with many other countries in that only 240 species of bird regularly breed or winter in the country (Appendix III), yet the total number of species which was recorded in Britain in the average year between 1980 and 1996 was 393, and fluctuated between 371 and 413 (Fig. 2.9). At the time of our visit to Eastern Wood, the total number of species ever recorded in Britain stood at 550. This figure represents species considered by the British Ornithologist's Union (BOU) to have occurred in Britain in a wild state, and thus excludes those for which a captive origin seems most likely. With an active trade in caged birds, of which a percentage are bound to escape, deciding which occurrences of unusual species in Britain constitute genuine instances of vagrancy is complicated and, to some degree, subjective (it is near impossible to *prove* either as the source of individual occurrences; Simpson 1991; Vinicombe *et al*. 1993; Parkin & Knox 1994; Holmes *et al*. 1998). For example, the same set of records as is judged by the BOU to provide evidence of the wild occurrence in Britain of 550 species is judged by Evans (1997a) to provide evidence for 580 wild species. Nevertheless, the important points are that this number is in the range 500–600, rather than, say, 100–200 or 1000–1100, and that the majority of the total species list for Britain comprises irregular visitors or vagrants. A large number of these have only been recorded at most a handful of times (Fig. 2.10).

In the period 1988–92, there were approximately 5500 records of individual vagrant birds in Britain. This is probably something of an underestimate of the numbers which actually occur. Fraser (1997) uses the phenomenon of 'weekend bias' to calculate these numbers. This refers to the tendency for vagrant birds to be discovered at weekends, when more birders are looking for them.

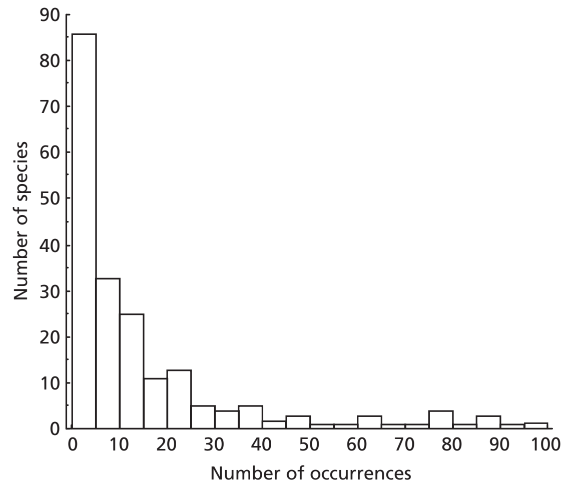

Fig. 2.10 Frequency distribution of the number of observed occurrences between 1958 and 1985 of the 204 species of bird for which less than 100 individuals of apparently wild origin were recorded in Britain in that period. From data in Dymond *et al*. (1989).

Fraser combined the assumption that 90% of all vagrants present on Sunday are detected by observers, with information on how many individuals are found on other days and how long vagrants tend to stay after they have been located, to estimate that almost half of all vagrant individuals to Britain go undetected. Given the frequency distribution of the number of occurrences of the rarest species (Fig. 2.10), some of the undetected vagrants will no doubt belong to species as yet unrecorded in Britain. The British bird list would undoubtedly be higher even than it is if all vagrants that made it to the country were discovered.

Whether the exact figure is 550 or 580, and whether or not this could have been higher had all vagrant individuals been discovered, the number of species recorded in Britain is relatively high for a country of its size and geographical position (intermediate latitudes, edge of a continent). In comparison, Evans (1997a) quotes totals for France and Italy of 515 and 491, respectively. The British list has the benefits of the efforts of the army of resident birdwatchers that make this particular avifauna so good for macroecological studies. Nevertheless, despite this huge contingent of observers, the list still compares poorly with those of many other countries. The species list for the Gambia, for example, stands at around 540 species (Barlow *et al*. 1997), but in a country less than 5% the size of Britain (Anonymous 1997). These figures compare with the 1080 species recorded from Kenya (Zimmerman *et al*. 1996), and the 1695 from Colombia (Hilty & Brown 1986).

Britain sits within the biogeographical region known as the Western Palaearctic. Evans (1997b) gives 938 as the number of bird species recorded from this region (again, the precise figure is debatable, depending on inclusion criteria, but it is the magnitude that is more important). Thus, a high proportion (≈60%) of the species recorded in this region have also been recorded in the small fraction that is Britain. The avifauna of the Western Palaearctic constitutes under 10% of the global total (Sibley & Monroe 1990, 1993). This compares with around 20% of the global total in Africa (Brown *et al*. 1982), and over 30% in South America (Rahbek 1997).

2.1.3 *Making sense of the numbers*

Over the last few pages, we have cited a large array of numbers, constituting species richness estimates for a wide range of areas of different size, scattered across the globe. These estimates are dynamic, increasing with time for reasons that change with temporal perspective. *The* species richness of an area does not, as such, exist. Nevertheless, since the rate of accumulation of species records usually quickly slows to a level at which additions are relatively rare occurrences (e.g. Figs 1.3 & 2.2), it is possible to compare the richness of different faunas, and ask why some are more speciose than others.

In that regard, as we have stepped up the scale ladder illustrated in Fig. 2.1, we have seen that the avifaunas of Eastern Wood, Britain and the Western Palaearctic are all poor relative to other avifaunas for which comparable data exist. However, while tiny in comparison to many local faunas around the

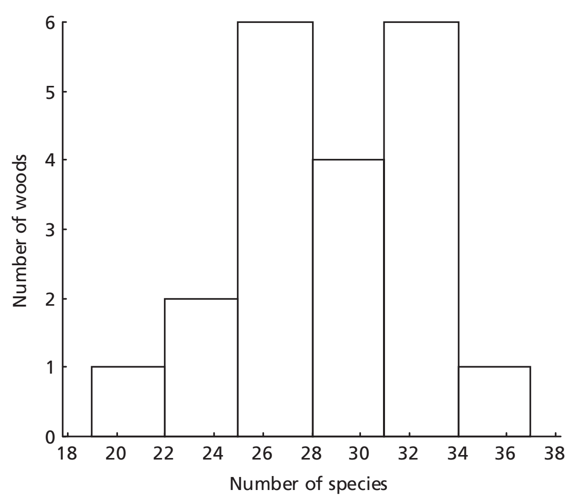

Fig. 2.11 Frequency distribution of the number of species of bird recorded in different woodlands, for a sample of 20 woodlands in southern England, including Eastern Wood. The number of species breeding in Eastern Wood is taken as the arithmetic mean over the 30 years of surveys. Data on the number of species breeding in the other woods are from Woolhouse (1983) and Ford (1987), but only include sites with area in the range 10–34 hectare, and concern a single year.

world, the avian species richness of Eastern Wood is not unusual for a deciduous woodland habitat in southern Britain. Figure 2.11 illustrates the number of bird species recorded breeding in one year in a sample of woods from southern England. Although the richness of Eastern Wood is towards the high end of this sample, it is well within its limits. But, why does it have the richness that it does? And why do other areas the world over have the richnesses they do? These are fundamental ecological questions. The answers encompass a range of different processes.

2.2 Size of area

One of the principal factors determining the number of species likely to be found at any site is its size. That species richness should be related to area is obvious. For example, there are close to 10 000 extant species of bird, but only 550 species have been recorded in Britain and Ireland (314 000 km^2) and 544 in Britain alone (230 000 km^2). Only 312 of the British species have been seen within the current boundaries of the county of Berkshire (1259 km^2; Standley *et al*. 1996), and only six within the current boundaries of T.M.B.'s urban Berkshire back garden (0.000075 km^2). The area within which the Eastern Wood assemblage has been censused is a mere 16 hectare (or 0.16 km^2), set within a larger tract of woodland that covers the approximately 112 hectare which comprise Bookham Common. This area is by no means small in comparison to other woodland patches in the highly fragmented region of southern England (cf. Moore & Hooper 1975; Woolhouse 1983; Ford 1987). Nevertheless, the number of birds recorded breeding in the wood is likely to be dictated foremost by its size. Indeed, the positive relationship between number of species found at a site and its area—the 'species–area' relationship—is one of the most robust and general patterns in ecology (Connor & McCoy 1979; Williamson 1988; Rosenzweig 1995).

More interesting than the existence of a species–area relationship is what form that relationship should take. This has been debated almost since the relationship was first documented (Arrhenius 1921, 1923; Gleason 1922, 1925; Connor & McCoy 1979; Wright 1981; Williamson 1988; Palmer & White 1994; He & Legendre 1996).

Debate about the shape of species–area relationships has centred on the transformation required to linearize them. Such transformation is desirable because linear relationships are easier to understand and compare than are curvilinear ones, and untransformed species–area relationships are rarely linear. In general, species numbers increase with area at a declining rate. Thus, as noted above, the number of breeding bird species in Surrey (≈1850 km^2) is 2.5 times that in Eastern Wood (0.16 km^2), but the total number breeding in Britain (≈230 000 km^2) is only about double that breeding in Surrey. Those studies that have compared the fits of different models to a wide variety of