

to avifaunas around the world argues that, at least initially, species are entering unsaturated communities.

The typically Type I relationship between local and regional richness means that to understand the determinants of local richness one must understand the determinants of regional richness. As argued from the opening chapter, the ecology of local assemblages cannot be understood without also incorporating a broader-scale perspective. Therefore, we now turn our attention to what is known about patterns in the species richness of regions, and to consideration of their likely causes.

2.5 Latitude

The effect of isolation identifies the position of a site such as Eastern Wood relative to other habitat patches as an important determinant of its species richness. However, richness may be affected not only by relative position, but also by absolute position in space because species distributions are not spread homogeneously across the planet. Some areas are richer than others. Moreover, the heterogeneity is not random. A number of consistent large-scale trends in richness can be identified. The first we will consider relates to latitude.

Across Britain, there is a marked cline in avian species richness. The highest levels are encountered in the south, and the lowest in the north (see, for

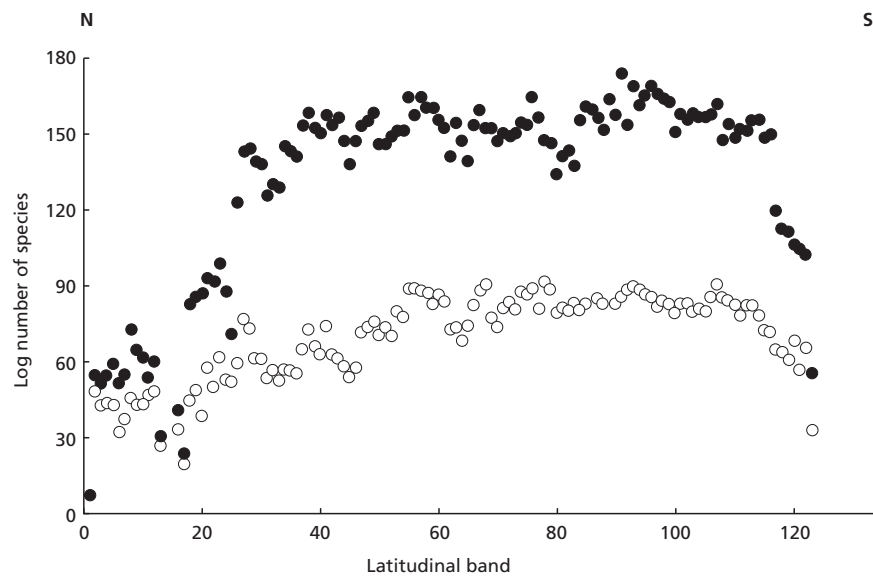


Fig. 2.26 The latitudinal pattern of breeding bird species richness across Britain, based on the mean number of species per 10 10-km grid cell in a latitudinal band (open circles) and the total number of species in each such band (filled circles). The decline in richness in the extreme south reflects the peninsula effect illustrated in Fig. 2.22. From data in Gibbons *et al.* (1993).

CHAPTER 2

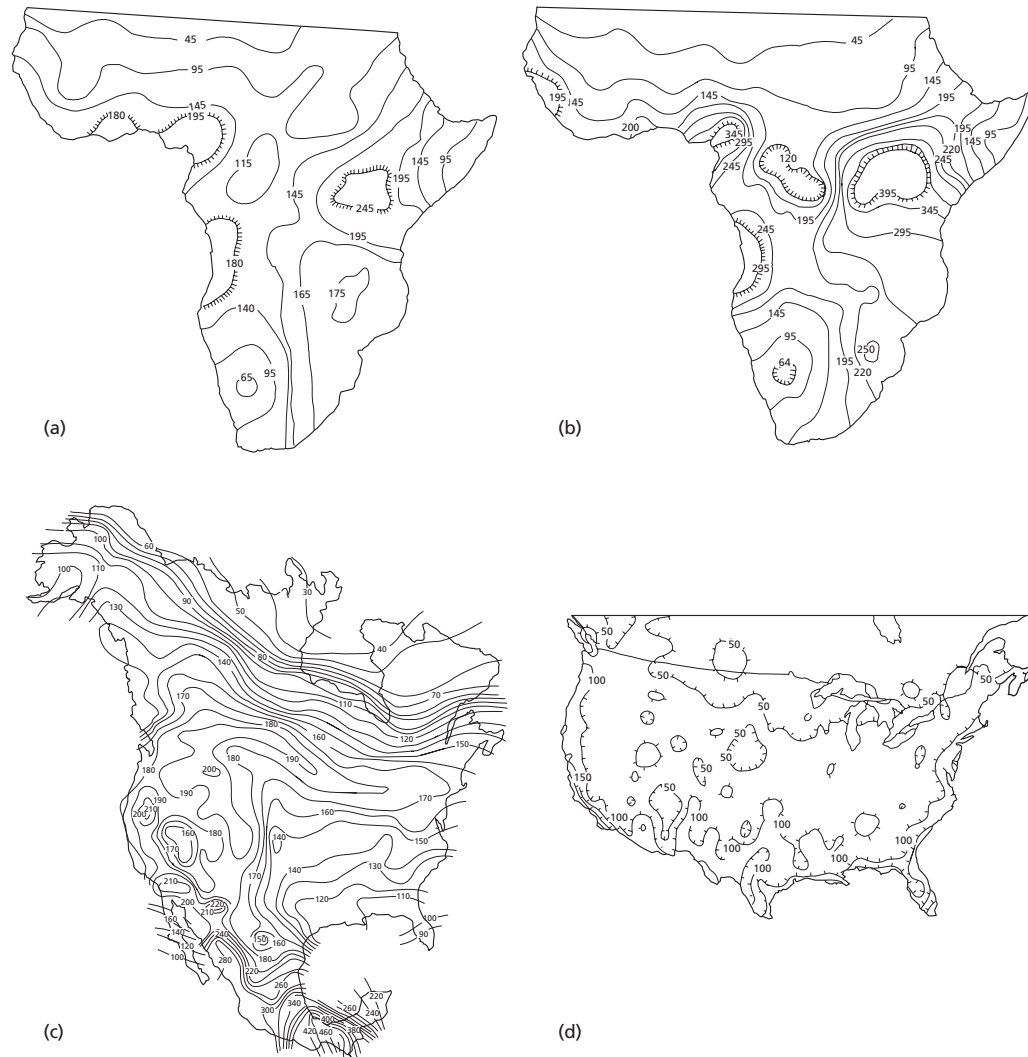
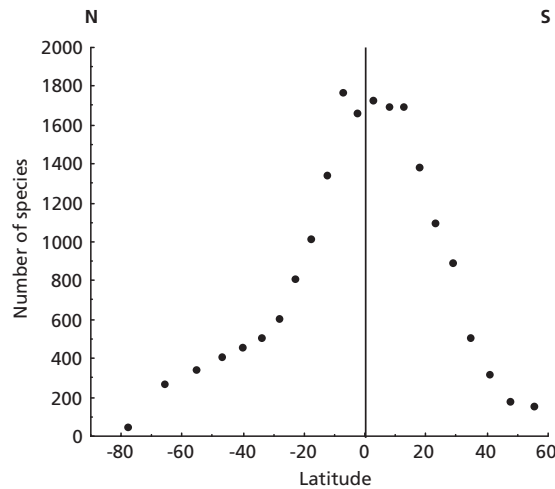


Fig. 2.27 Geographical variation in numbers of species for (a) non-passerines and (b) passerines in the Afrotropics, and (c) breeding and (d) wintering birds in the Nearctic. From Cook (1969, with permission from Taylor & Francis), Crowe and Crowe (1982, with permission from Cambridge University Press) and Root (1988a, with permission from University of Chicago Press).

example, Fig. 2.26, and maps in Sharrock 1976; Fuller 1982; Lack 1986; Turner *et al.* 1988; Gibbons *et al.* 1993; Williams 1996a; Williams *et al.* 1996; Williams & Gaston 1998). This is true not only for the avifauna as a whole, but also for the communities occupying different habitats (Fuller 1982), which means that it is not a simple consequence of a latitudinal cline in habitat diversity. Hence, the high richness of Eastern Wood relative to other British woodlands may be in part because it lies near the extreme south of the region.



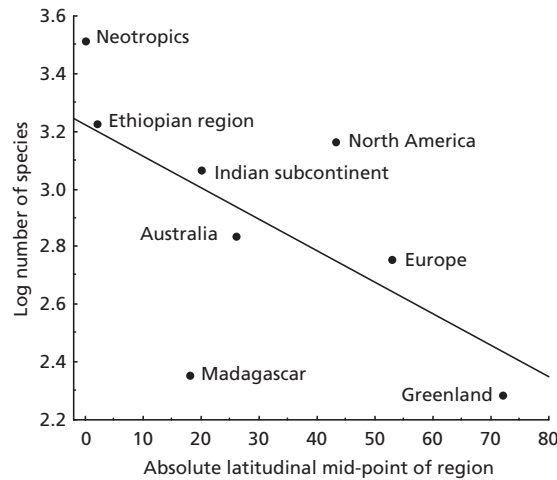


Fig. 2.29 The relationship between number of species and latitude (degrees) for birds in different biotic regions ($y = 0.011x + 3.22$; $r^2 = 0.41$, $n = 8$, $P = 0.087$). From data in Slud (1976), as used in Fig. 2.16.

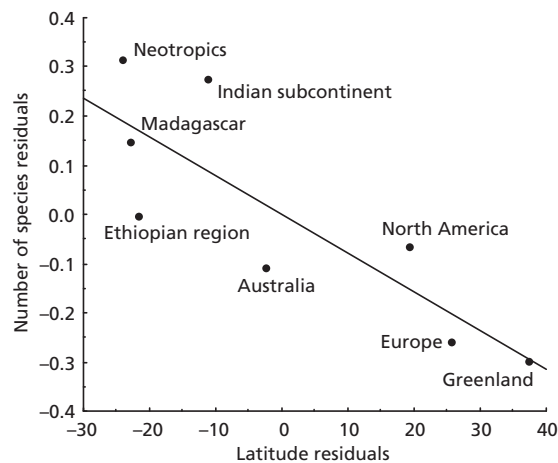


Fig. 2.30 The relationship between number of species and latitude for birds in different biotic regions, controlling for the effects of land area ($y = 0.008x$; $r^2 = 0.70$, $n = 8$, $P = 0.009$). For a given land area, regions centred at low latitudes have higher species richness than regions centred at high latitudes. The axes are the residuals of plots of \log_{10} species richness against \log_{10} area (km^2) and of regional absolute mid-latitude (degrees) against \log_{10} area. Area and richness data were taken from Slud (1976), as used in Fig. 2.16.

However, the difference is slight, and at present the jury is out on the question of its broader generality (Gaston 1996b; Gaston & Williams 1996).

Although the latitudinal richness gradient is one of the most consistent ecological patterns, there are still exceptions. Thus, while most major taxa exhibit a gradient, the same is not true of all their constituent subtaxa. For birds, this is

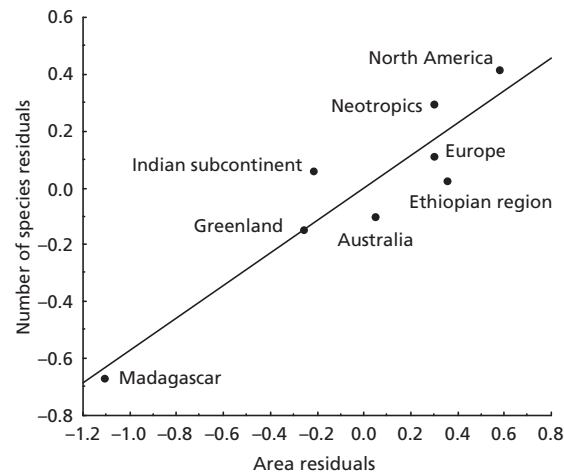


Fig. 2.31 The relationship between number of species and area for birds in different biotic regions, controlling for the effects of latitude ($y = 0.57x$; $r^2 = 0.86$, $n = 8$, $P = 0.001$). For a given regional absolute mid-latitude, larger regions have higher species richness than smaller regions. The axes are the residuals of plots of \log_{10} species richness against regional absolute mid-latitude (degrees) and of \log_{10} area (km^2) against regional absolute mid-latitude (degrees). Area and richness data were taken from Slud (1976), as used in Fig. 2.16.

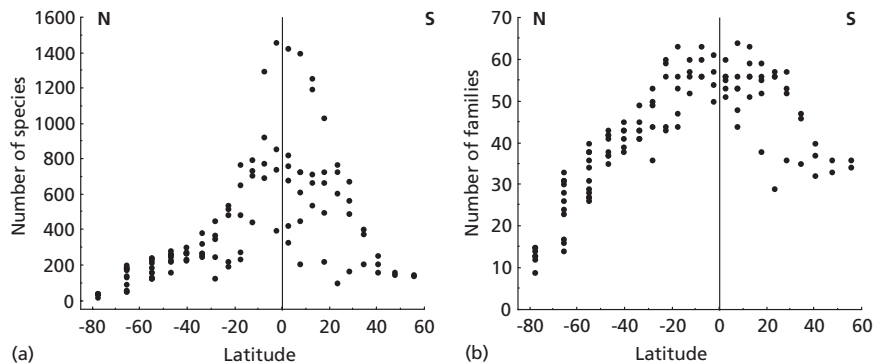


Fig. 2.32 The relationship between (a) number of species and (b) number of families and latitude (degrees) for birds in the New World. Each point represents the number of species or families recorded (breeding or wintering) in each square on the WORLDMAP grid (a cylindrical projection of the world divided into equal-area squares, each approximately $611\,000\text{ km}^2$, for intervals of 10° longitude, and symmetrical about the Equator; Williams 1992, 1993), and the latitudinal mid-point of that square. The Equator is indicated by a vertical line.

in most cases a trivial consequence of the observation that some taxa are adapted to life at higher latitudes (e.g. penguins and auks). More significant and interesting exceptions exist for other taxa: aphids, sawflies, ichneumonids and bees all show richness peaks at intermediate or high latitudes (e.g. Owen

& Owen 1974; Michener 1979; Janzen 1981; Gauld 1986; Dixon *et al.* 1987; Roubik 1992; Williams 1993; Kouki *et al.* 1994; Williamson 1997). Other taxa may show a gradient in some regions but not in others. Thus, Nearctic and Palearctic mammals increase in richness towards low latitudes (Pagel *et al.* 1991a; Letcher & Harvey 1994), but Australian mammals do not (Smith *et al.* 1994). The total richness of birds appears to be highest at mid-latitudes within Europe (Mönkkönen 1994; Gregory *et al.* 1998) and Australia (Schall & Pianka 1978; Blakers *et al.* 1984; Pearson & Cassola 1992). No obvious latitudinal richness gradient is shown by birds in Ireland, where centres of highest richness are at mid-latitudes (Gibbons *et al.* 1993). These variations may be useful for distinguishing between potential explanations for richness gradients.

2.5.1 *Why oh why?*

The answer to why there are more species at lower latitudes has long been a puzzle. An obvious starting point is that the pattern has no biological basis at all, but is instead a consequence of random location of species distributions across latitudes. Colwell and Hurtt (1994) have shown that this mechanism can produce species richness gradients as long as there are hard (i.e. impermeable) boundaries that limit species distributions. Because latitudinal gradients tend to have hard boundaries, imposed generally by the Poles, or by land's end for terrestrial species, this is a reasonable condition. Whether this model can explain real latitudinal richness gradients is currently unclear, as it has not yet been widely tested. The only studies that have compared the model against data conclude broad support for its predictions (Lees 1996; Willig & Lyons 1998; Lees *et al.* 1999), but we are not convinced that the results are indicative of a general explanation for latitudinal richness gradients. Thus, while the random model explains reasonable amounts of variation in marsupial and bat species richness across latitudes in the New World (Willig & Lyons 1998), this is hardly surprising given that both real and model gradients peak near the Equator; the pattern of increase with latitude is quite different between the two. Nevertheless, the extent to which random models explain latitudinal gradients awaits further study, and we anticipate that they will play an increasingly major role in studies of species richness gradients.

In addition to the random model, more than a dozen separate explanations for latitudinal richness gradients have been proffered, based on such diverse factors as environmental stability or predictability, environmental patchiness, competition, predation, parasitism, mutualism, productivity, solar energy and latitudinal patterns in geographical range size (numerous reviews and discussions include Fischer 1960; Pianka 1966; MacArthur 1969, 1972; Ricklefs 1979; Shmida & Wilson 1985; Platnick 1992; Rohde 1992; Rosenzweig 1992, 1995; Latham & Ricklefs 1993; Ricklefs & Schluter 1993; Begon *et al.* 1996; Blackburn & Gaston 1996c; Gaston & Williams 1996; Williamson 1997). We do not intend

to re-examine all these possibilities here: that process would be a book in itself, especially as it is likely that many of the mechanisms proposed may help to explain the details of richness gradients in some taxa in some situations (Williamson 1997). Rather, we will concentrate on the three attempts to cut the Gordian knot which seem to us to offer the most general promise. While selecting for detailed attention just three of the explanations for latitudinal richness gradients might seem arbitrary, there are good reasons to do so, apart from their popularity in the literature. These will be clearer following Chapter 6.

2.5.2 *Area again*

One remarkably simple hypothesis is that the tropics has the highest species richness because it has the greatest geographical area; the 'geographical area hypothesis'. This idea originates with Terborgh (1973; see also Schopf *et al.* 1977; Osman & Whitlatch 1978), but has principally been championed by Rosenzweig (1992, 1995; Rosenzweig & Sandlin 1997). Large geographical area may translate into high species richness through the effect of area on the geographical range size attainable by species in different regions. Species inhabiting spatially extensive regions can have larger geographical ranges than can those inhabiting more restricted regions. Species with larger ranges are buffered against extinction from accidental causes, because they are more likely to have large population sizes, and against extinction from environmental perturbation, because they are less likely to have their entire population affected. Conversely, species with large ranges may be more susceptible to allopatric speciation through the formation of geographical barriers, which may isolate subsets of their total population (but see Chapter 3). Since speciation rates may be raised and extinction rates reduced in regions of greater spatial extent, these regions should also have higher levels of species richness (Rosenzweig 1992, 1995).

It should be clear that this explanation for the effect of area on species richness is couched in terms quite distinct from that of our earlier discussions of species–area relationships. This is simply because the areas of concern are so large. Four processes ultimately determine variation in species numbers in any area: speciation, extinction, immigration and emigration. For these very large areas, speciation and extinction (at the whole-species level) predominate, and immigration and emigration are less important. For very small areas, immigration, emigration and local extinction predominate, and speciation and species-level extinction are very unlikely.

Considering only the terrestrial environment, the tropics is the most extensive of the biomes (areas of relatively homogeneous environmental conditions), and so should, on the basis of the geographical area hypothesis, have the highest richness, which indeed it does. However, successive biomes (as defined in Rosenzweig 1992) north of the tropics all have about the same land area. If the

geographical area hypothesis is correct, these regions should all have approximately the same species richness. That they do not could result, at least in part, from the ranges of tropical species extending out into neighbouring biomes. This effect should be stronger in those biomes closest to the tropics, giving rise to a 'secondary' latitudinal richness gradient. Rosenzweig (1992, 1995) suggested that if species with partly tropical distributions were excluded, the richness gradient north of the tropics should disappear. By extension, the strength of the richness gradient across biomes south of the tropics should also depend on the relative land areas of those biomes once tropical species have been excluded, although the predictions for both hemispheres may be tempered by the general decrease in the productivity of the environment at higher latitudes. Blackburn and Gaston (1997a) tested the effect of removing tropical species on latitudinal patterns in avian species richness in the New World. They found that there is indeed a relationship between the land area and the species richness of a biome once predominantly tropical species are excluded.

The geographical area hypothesis potentially explains why we see large-scale patterns in bird species richness across the globe. It provides one reason why the richness of Eastern Wood is lower than that, for example, for Kakamega Forest in Kenya. However, it is difficult to use the geographical area hypothesis to explain the existence of a latitudinal gradient in avian species richness within Britain, and hence to explain why the latitude at which it lies contributes to the numbers of species occurring in Eastern Wood. This is not so surprising. As just noted, the geographical area hypothesis explains large-scale richness patterns. Additional processes, such as those discussed above, are likely to fine tune the details within the broad patterns. For example, the avian species richness gradient within Britain may in part result from the greater isolation of northern areas from the continental source pool (Section 2.3). The geographical area hypothesis may contribute to the effect in that the source pool for many southern species (e.g. nuthatch, lesser whitethroat, hawfinch) may be the European temperate biome, whereas the source of many northern species (e.g. ptarmigan, dotterel, snow bunting) may be the poorer boreal biome. Thus, the richness of Eastern Wood may compare unfavourably with other woodland sites around the world as a consequence of the size of the area from which it draws its species, but favourably with woodland sites in Britain for other reasons. However, one of these other reasons also has the potential to explain large-scale gradients in species richness, and we consider it next.

2.5.3 *Energy*

Alongside area, the other strong contender as an explanation of latitudinal variation in species richness is the 'energy hypothesis'. Put baldly, this states that higher energy availability in an area provides a wider resource base,

permitting more species to occur there (Tilman 1982; Wright 1983; Turner *et al.* 1987, 1988, 1996; Currie 1991; Wright *et al.* 1993). In fact, there is absolutely no reason at all why *per se* this should be so (Currie 1991; Rohde 1992; Blackburn & Gaston 1996c), and the hypothesis requires some more detailed embellishment to make it clear.

At the upper limit, the absolute amount of life on Earth (hydrothermal vent and other chemolithotrophic communities excluded) cannot exceed that which can be supported by the harnessing of all energy arriving from the sun. Because some energy is conducted and convected away from the region in which it first falls, not all can be converted. Since initial plant, and subsequent animal, conversion efficiencies are less than perfect (i.e. 100%), the absolute upper limit will inevitably be still lower than that expected from levels of solar radiation alone. Effectively, this energy is converted to biomass, or some number of individuals. The way in which this biomass or these individuals are 'divided up' into species then determines the species richness of an area. Energy levels may dictate how much biomass (say) there is to be allocated, but seem unlikely to mediate the allocation process (Blackburn & Gaston 1996c). Nevertheless, it is relatively easy to construct an argument explaining why energy-rich areas should also be species rich, based on simple assumptions about speciation and extinction (Turner *et al.* 1996).

First, speciation is assumed to be a stochastic process, operating in the same way at all latitudes. This would generate equal diversities across the globe. The exact process by which speciation occurs is unimportant for this argument, but it is important that some speciation does happen. If it does not, then one species simply monopolizes all available energy. Reasons why speciation would be expected in any given biogeographical region can easily be posited. Most obviously, no single species can master all ways of life, and different strategies are likely inevitably to lead to speciation. Second, extinction is assumed to be inversely related to population size. Given these two assumptions, more species are expected to persist where extinction is lowest, which will be in areas where species have larger population sizes. These should be areas with higher levels of energy input (Turner *et al.* 1996), where more biomass can be sustained, and hence where larger population sizes may be expected for a given number of species (or, looked at the other way round, where more species may sustain populations above some critical size).

These ideas beg a number of important questions, and we will return to some of these at various places later in the book (especially Chapter 6). At this point, the important issue is whether energy and species richness are related in a way which can explain latitudinal gradients in species richness.

A large number of studies have documented relationships between species richness and estimates of energy availability. As energy availability is reasonably difficult to measure directly, these studies typically use surrogate measures, the principal of which is primary productivity. Productivity is assumed

to reflect the input of solar energy because it is only plants that can use this energy to produce biomass. Clearly, energy input and primary productivity are not perfectly related, as there are many parts of the globe that receive plenty of energy with little resultant plant growth, due to the lack of other essential elements (principally water). Nonetheless, their relationship may be sufficiently close for general purposes. The other major surrogates for energy availability are measures of climatic variables.

Studies of the relationship between energy availability and species richness tend to fall into two broad groups. On the one hand, there are those which report hump-shaped relationships, in which species richness peaks at intermediate levels of energy availability or productivity (Grime 1973; Al-Mufti *et al.* 1977; Tilman 1982; Abramsky & Rosenzweig 1984; Owen 1988, 1990; Kerr & Packer 1997; Guo & Berry 1998; Chown & Gaston 1999a). On the other hand, there are studies which report broadly positive relationships, in which species richness peaks at the highest levels of energy availability, or in the warmest climates (Wright 1983; Turner *et al.* 1987, 1988, 1996; Adams & Woodward 1989; Currie 1991; Wylie & Currie 1993a,b; Blackburn & Gaston 1996b; Fraser & Currie 1996). Wright *et al.* (1993) observe that variation in the shape of the relationship depends on the spatial scale of study, with hump-shaped relationships observed at smaller scales and positive relationships at larger ones. They suggest that this scale dependency implies that different factors control richness at different scales, with energy important at large spatial scales.

One notable exception to the generalization by Wright *et al.* about scale dependency is a study by Chown and Gaston (1999a). They mapped the distribution of all Procellariiformes (albatrosses, shearwaters, petrels, storm-petrels, diving-petrels) onto an equal-area grid covering the world's oceans, and found a hump-shaped relationship between the species richness of grid squares and estimates of productivity. Thus, the richest areas of ocean do not hold the highest numbers of seabird species.

Chown and Gaston suggested two reasons why a hump-shaped richness-productivity relationship might occur in this system. First, they noted that highly productive areas of ocean cover smaller geographical areas than do areas of intermediate productivity, while local and regional seabird species richness are positively correlated. Thus, the hump-shaped relationship may arise because larger areas support more species in total, despite having lower productivity per unit area, while regional richness elevates local richness, as we saw earlier (Section 2.4). Second, Chown and Gaston noted that highly productive areas of ocean also tended to exhibit higher temporal variability in productivity. Thus, highly productive areas may have lower species richness because seasonality in production prevents exploitation of those areas by seabirds for substantial periods of the annual cycle. Supporting this second idea is a negative relationship between procellariiform species richness and geographical range size: seabirds with small range sizes cannot persist in areas

with highly seasonal productivity, which cannot support their populations all year round.

Additional evidence presented by Chown and Gaston (1999a) seems to suggest that the second of these two explanations for the hump-shaped richness–productivity relationship is the most important in this system. This led them to propose a general explanation for when hump-shaped relationships should occur, and when such relationships should be positive. When productivity and its variance are positively correlated, hump-shaped relationships should pertain, because productive areas will not be able to maintain high species richness all year round. However, positive relationships between richness and productivity should be found when productivity and its variance are negatively correlated.

At the scale of Britain, Turner *et al.* (1988, 1996) have shown that patterns in bird species richness fit well with predictions of the energy availability hypothesis. In particular, they compared predictors of the richness of species between seasons. They argued that if climate (and hence energy) is an important predictor of avian richness, then different patterns of species density should pertain in summer and winter, as the principal temperature gradient runs north–south in Britain in summer, but in winter has a much stronger east–west component. In essence, this is what they found. However, the exact patterns were modified by body size (see Cousins 1989). Winter temperatures affected the distributions of species of all sizes, whereas summer temperatures only affected the distributions of the smallest species (Turner *et al.* 1996). Turner *et al.* suggested that this further supports the energy hypothesis, as all species should suffer from temperature stress in winter, whereas only small-bodied species are likely to be susceptible to such stress in summer.

These energetic arguments might suggest why the breeding bird richness of Eastern Wood is low relative to many places in the world, but high relative to other British woodlands. Latitudinal gradients in energy availability could generate both of these observations, because Eastern Wood is a long way from the Equator (where energy availability ought to be highest), but not as far from the Equator as is most of Britain. Energy may therefore dictate the number of species that Eastern Wood can support.

One obvious deficiency with energetic arguments such as that propounded by Turner *et al.* (1988, 1996) is that while energy does a good job of explaining patterns in the modern-day distribution of British birds, very few of those species are likely actually to have evolved in Britain. Indeed, just a few thousand years ago most of the country was covered by a thick layer of ice. Thus, while the results reported by Turner *et al.* can explain the current distribution of bird richness, they do not necessarily say anything about the factors that drove the evolution of that richness. On the other hand, they do illustrate an association between energy (climate) and richness that needs explanation. That the association might be causal is not improbable.

The fact that Britain was until relatively recently covered by glaciers highlights an important additional consideration with respect to theories of the evolution of species richness. The richness of an area will ultimately depend on the processes of speciation, extinction, immigration and emigration. However, all these processes take place in time. Large, energy-rich areas will be species poor if there has been little time for speciation or immigration to have occurred. In the extreme, of course, the planet was species poor early on in evolutionary history. This has led to a third popular explanation for latitudinal gradients in species richness, that they are dependent on the amount of time available for the processes of speciation and colonization to have occurred at different latitudes.

2.5.4 *Time hypotheses*

Time hypotheses can loosely be split into that concerning ecological time and that concerning evolutionary time (Pianka 1966). The ecological time hypothesis proposes that the low richness of some regions is a consequence of the insufficient period available for species to colonize or recolonize since an earlier ecological upheaval. Adams and Woodward (1989) examined reasons for the well-known difference in tree species richness between North America, Europe and eastern Asia. The tree flora of Europe is depauperate relative to the other two regions. They showed that most of the variation could be explained by differences in productivity between regions: European areas had no fewer tree species than expected on the basis of their productivity. However, Adams and Woodward also noted unexpected regional differences in tree richness in the most productive areas, with these attaining higher richness in eastern Asia. The bird species richness of eastern Asia, eastern North America and the Western Palaearctic mirrors the pattern exhibited by trees. Thus, the avifauna of the Western Palaearctic is depauperate relative to the other two regions (Blondel & Mourer-Chauviré 1998), and this is particularly true of the bird communities associated with forest (Mönkkönen & Viro 1997). Adams and Woodward (1989) and Blondel and Mourer-Chauviré (1998) both attributed these differences to the effects of glaciation in the three regions. They suggested that glaciation resulted in higher levels of extinction in the Western Palaearctic because the predominantly east–west orientation of geographical barriers there (e.g. the Alps, Mediterranean Basin and Sahara Desert) prevented northern species from retreating south as the glaciers advanced, and then prevented southern species from recolonizing as the glaciers retreated. In effect, they are arguing that the numbers of tree and bird species present in high productivity areas in Europe and North America have not regained their preglaciation levels.

In the case of Eastern Wood, avian richness might be low because recolonization of Britain by bird species since the last glaciation is still in progress.

Because this recolonization would inevitably proceed from the south, the process would also explain the richness gradient across Britain. However, while this mechanism can potentially explain small-scale richness patterns, it is unlikely to provide a general explanation for latitudinal richness gradients. The question of what generates the number of species available for recolonization remains.

An answer to this question seems more likely to derive from an evolutionary time hypothesis. This suggests that the richness of regions relates to the length of time available for species to evolve to fill habitats and niches in those regions. As such, it deals with longer spans of time than the ecological time hypothesis, and focuses on speciation, rather than colonization. It proposes that large-scale upheavals, such as glaciation or climatic drying, periodically drive extinct many of the species in a region, and that the floras and faunas of those regions exposed to more frequent upheavals have less time to rediversify. This leads to regional differences in species richness. The mechanism also fits well with the opportunistic view of ecological communities espoused in the opening chapter, as it implies that most communities are likely to be unsaturated collections of species, and thus open to additional species invasions (see also Järvinen & Ulfstrand 1980).

Some evidence for the effect of evolutionary time on richness has been produced by Rohde (1978, 1986, 1992, 1997). He noted differences between the Atlantic and Indo-Pacific oceans in the species richness of both fish and their monogenean gill parasites, with richness higher in the latter region. He reviewed explanations, and concluded that evolutionary time was the most likely. Latham and Ricklefs (1993) argued that the patterns of tree species richness analysed by Adams and Woodward (1989) might be better understood if the effects of evolutionary time on richness were considered.

If the evolutionary time hypothesis is correct, it implies that more time should have been available in the tropics to have allowed so much additional net speciation to have occurred there. Rohde (1992) argues that this is not the case, as short- and long-term fluctuations between warm and cold states have occurred in the global climate for the past 700 million years (Fischer 1981). However, he goes on to suggest that what is important is not the absolute amount of time available at different latitudes, but the effective evolutionary time. This will be a product of absolute time and the rate at which the evolutionary process occurs. Rohde argues that it is this rate that is likely to differ across latitudes as a consequence of the effect of climate, leading to the higher richness of the tropics.

Whether or not an evolutionary time hypothesis based on effective rather than absolute time is an improvement remains to be demonstrated. In particular, it is as yet unclear whether evolutionary rates are indeed faster in the tropics (Rohde 1997), as the hypothesis suggests. Also, quite why fluctuations in the global climate across all latitudes *per se* should count against the

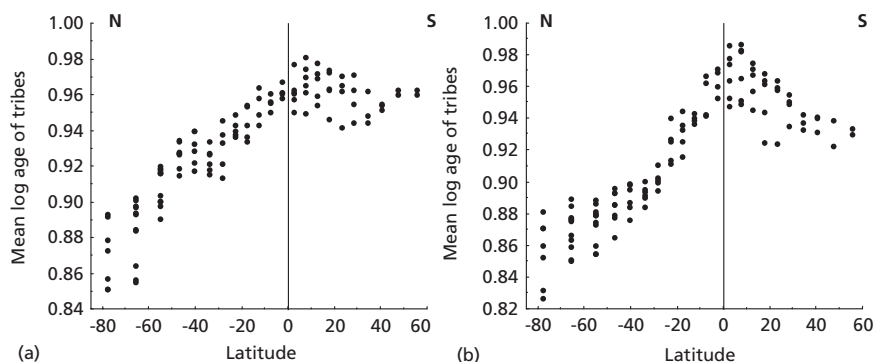


Fig. 2.33 The relationship between the mean age of avian tribes (from data in Sibley & Ahlquist 1990) and latitude (degrees) for birds in the New World. Each point represents the mean of the \log_{10} -transformed ages of tribes in each square of the WORLDMAP grid (see Fig. 2.32 for details), and the latitudinal mid-point of that square. In (a) tribes are unweighted, and in (b) are weighted by the number of species of each tribe present in the square. The Equator is indicated by a vertical line. From Gaston and Blackburn (1996b).

evolutionary time hypothesis is unclear to us. What matters is the magnitude of these fluctuations at different latitudes, and they are surely likely to be more severe at latitudinal extremes (e.g. Fischer 1981). Moreover, a fascinating result for birds suggests that there are genuine latitudinal differences in the long-term persistence of taxa. Gaston and Blackburn (1996b) showed that the mean age of tribes and families inhabiting different latitudes in the New World was highest at the Equator (Fig. 2.33). While this pattern can be produced by a variety of different latitudinal patterns of speciation and extinction rates (including, paradoxically, higher extinction rates in the tropics: Gaston & Blackburn 1996b), it is perhaps most likely to show that tropical bird taxa have persisted for longer periods of time, as the evolutionary time hypothesis predicts. That conclusion agrees with other more fine-scale analyses of the distribution of avian species of different ages in South America and tropical Africa, which indicate that lowland tropical forests act as 'sinks' where species accumulate over time (Fjeldså 1994).

2.5.5 A 'primary cause'—holy grail or wild goose?

Implicit in what we have said about latitudinal gradients in richness has been the idea that some explanations can account for some patterns. A good example is the ecological time hypothesis. However, an assumption common to many discussions of the determinants of these gradients is that no mechanism can be supported unless it explains the patterns in all taxa and in all regions. That is, that there is one primary cause of the increase in species richness from high to low latitudes, and any study that unequivocally rules out a mechanism in one region of the globe automatically rules it out in all others. This view

is exemplified by MacArthur and Connell's (1966) general statement that: '(w)herever there is a widespread pattern, there is likely to be a general explanation which applies to the whole pattern'.

There is, however, no logical reason why this need be so. To argue for a single primary cause may be to expect a simplicity from ecological interactions for which there is little evidence, and a number of authors have pointed out that observed ecological patterns are likely to be generated by several contributory mechanisms (Wilson 1988; Warren & Gaston 1992; Blackburn & Gaston 1996b,c; Jablonski 1996a; Lawton 1996a; Gaston *et al.* 1997a; Williamson 1997; Gaston & Blackburn 1999). Moreover, Lawton (1996a) has suggested that the strongest and most general patterns are those where all the different mechanisms pull in the same direction: generality is not evidence for primary cause.

In this regard, it is interesting to note the similarities in the geographical area and energy availability hypotheses. The geographical area hypothesis assumes that area influences richness through its effect on geographical range size, which in turn influences rates of speciation and extinction. The energy availability hypothesis explicitly assumes that area influences richness through the effect of energy on population size, which in turn influences extinction rate. As we will see later (Chapter 4), though, there is good evidence that the geographical range size and abundance of species are generally positively correlated. Any factor that increases one of these variables will also be likely to increase the other. Therefore, the geographical area and energy availability hypotheses may be rather closely related. Both depend, in effect, on some factor that is posited to influence the biomass available to be worked on by the processes which ultimately determine how many species there are: speciation and extinction. However, this biomass will be a product of both area and available energy per unit area (Wright 1983; Wright *et al.* 1993): presumably, it is for this reason that small areas tend to be species poor however high their energy input, whereas large areas tend to be species poor if there is low energy input (cf. Madagascar and Greenland; Fig. 2.29). Therefore, both area and energy are likely to be important in determining large-scale patterns in the richness of species. Their effects are likely to be modified to some degree by the effects of effective evolutionary time. Whether effective evolutionary time is greater in the tropics because of latitudinal variation in evolutionary rates or climatic stability, real gradients in evolutionary time across latitudes would serve to enhance the resulting gradients in richness (Wilson 1992).

2.6 Longitude

The latitudinal richness gradient is a widely reported phenomenon, and has received significant attention from ecologists. By contrast, the tendency for richness to vary with longitude has been largely ignored, although it has long been appreciated. Indeed, Fuller (1982; p. 88) noted that the 'tendency for bird