and productivity in the horizontal dimension discussed earlier. Productivity is perhaps the more likely of the two explanations. The artefact hypothesis predicts that richness should peak at mid-elevations, whereas the peak is generally at low elevations, even when not at the lowest. However, Rahbek (1997) cites evidence that the relationship between productivity and altitude may itself not be linear, and sometimes show a peak at mid-elevations. If so, a direct productivity–richness relationship may pertain, and its variation be explained by variation in the form of productivity–altitude relationships.

2.8 Summary

The number of species recorded at a local site is not bounded, but depends on the time period considered. In part, temporal changes in richness are a consequence of sampling effort, with fewer of the species present being overlooked in longer, more thorough surveys. However, allowing for sampling effort, recorded levels of richness would be expected to increase through time due to faunal changes associated with such factors as seasonality, colonization and extinction, and, ultimately, speciation. Attempts to understand patterns of species richness need to take account of the time period over which the richness data have been assembled.

That said, the determinants of the species richness of a site like Eastern Wood are reasonably well known. They present a complex amalgam of processes acting at a variety of spatial and temporal scales. Consideration of processes at all scales will be vital for a complete understanding of the causes of observed richness patterns at local sites.

The habitats of which the site is composed determine in the first instance which species can make a living there. However, how many species do make such a living depends additionally on a broader set of factors.

At the smallest scales, the size of a site affects how many species it is likely to support. Size seems to exert its influence here through its positive relationship to the number of different habitats that the site encompasses, together with its effect on rates of immigration into and extinction from the site. More habitats mean more species. Larger sites are more likely to be located by immigrants, and support larger populations of those species that do locate the site, which as a consequence are less likely to be driven extinct by the vagaries of chance. The likelihood of colonization is also affected by the isolation of the site, with fewer immigrants locating isolated sites. Species in isolated sites will also have higher extinction rates because stochastic population declines are less likely to be rescued by influxes of immigrants. Thus, small, isolated sites will tend to contain fewer bird species than larger, less isolated sites, even if the sites are composed of equivalent habitat.

The size and isolation of local sites affect how they sample the avifauna of the region in which they reside, but features of that region are just as important.

Therefore, sites that are embedded within species-rich regions are likely to sample more species, and so themselves be richer, than are sites of identical size, isolation and habitat embedded within species-poor regions. Regional species richness is itself most obviously related to the latitude at which the region sits, although there are additional effects of longitude and altitude. The reasons for latitudinal variation in species richness are contentious, but are most likely to relate to variation in the area and productivity of regions, which together determine how much life (e.g. biomass) a region can support, and to variation in the effective amount of time available for the processes that divide that biomass up into different species. Thus, speciose regions ought to be those that are large, productive, and have had greater effective time for their floras and faunas to diversify. Deficiencies in any of these variables ought to reduce a region's richness. The least well-understood link in this argument at present is that relating to diversification: why should there be more species where levels of biomass are higher, and not just more individuals of a few generalist species?

This chapter has been unashamedly biased. It has emphasized large-scale processes as determinants of species richness, but has largely ignored many of the small-scale processes, such as competition, apparent competition and predation, that help determine how many species can co-occur together at any given site. We believe that this bias is wholly justified. It is large-scale processes that determine in the first instance how many species may be expected at a site. Small-scale processes fine tune their interactions. We hope that this chapter has convinced readers of the importance of a large-scale perspective for understanding ecological patterns, because it is for patterns of richness that this perspective is most readily appreciated. For the remainder of the book we move on to consider patterns for which the large-scale perspective is equally useful, but less well appreciated.