

recorded in the wood is significantly lower than predicted by this model. Thus, we can conclude that the sampling hypothesis cannot fully explain patterns in avian species richness in Eastern Wood.

Given that a pure sampling hypothesis generally cannot explain species–area relationships, we can turn attention from the null hypothesis, which is also falsified in this particular case, to biological explanations for the pattern. Principal among these is the habitat hypothesis (Williams 1964). Put simply, larger areas might contain more species because they contain more habitats. While, as just argued, the avifauna of Eastern Wood is likely to be composed only of species typical of deciduous woodland and its margins, the avifauna of Britain can include species reliant on open country (e.g. stone curlew, skylark), coniferous woodland (e.g. crested tit, common crossbill), fens (e.g. bittern, bearded tit), rivers (e.g. kingfisher, dipper, grey wagtail), lakes (e.g. grebes, ducks), saltmarshes (e.g. redshank) and moorland (e.g. red grouse, ring ouzel) (Fuller 1982). None of the species listed is likely to breed in Eastern Wood unless major changes in the habitat ensue. As long as species show some degree of habitat specialization, as is clearly true for British birds (e.g. Fuller 1982), Britain as a whole will have more species than Eastern Wood because it encompasses more habitats. In general, the species richness of larger areas may be higher for this reason.

The habitat hypothesis generates two obvious predictions: habitat diversity should be a better predictor of species richness than area, and there should be no species–area relationship (or, at least, not one that differs from the null hypothesis) in cases where increases in area are not accompanied by increases in number of habitats. Several studies support the first of these predictions (see also Johnson 1975; Boecklen 1986). For example, Reed (1981, 1983, 1984) showed that the number of habitat types on British coastal islands was a better predictor of the number of breeding landbirds than was area. Similarly, Haila (1983) noted that the number of bird species in communities of equal size was higher on those islands of the Finnish Åland archipelago with more diversified habitats (but see Martin & Lepart 1989). Rafe *et al.* (1985) found that a measure of habitat diversity was a better predictor than area of the number of bird species on a selection of Royal Society for the Protection of Birds (RSPB) reserves. Peck (1989) found a positive relationship between the number of bird species using compartments in a forestry plantation in northern England and the number of tree species in those compartments, while the number of tree species was not correlated with compartment size. Further evidence in support of the importance of habitat diversity has been found for a variety of taxa (e.g. Kitchener *et al.* 1980a,b; Rigby & Lawton 1981; Buckley 1982; Tonn & Magnuson 1982; Fox 1983; Haila & Järvinen 1983; Quinn *et al.* 1987; Sfenthourakis 1996; Burnett *et al.* 1998; Nichols *et al.* 1998).

Nevertheless, a number of studies have failed to support the first prediction of the habitat diversity hypothesis. McCollin (1993) found that the avian

richness of woodland fragments in east Yorkshire depended on between-patch (landscape) rather than within-patch (habitat) structure. Ford (1987) showed that area was the primary determinant of richness in Oxfordshire woodland islands, although habitat heterogeneity did explain significant amounts of residual variation in richness, and was the best predictor of richness in his control plots (embedded in larger areas of woodland). Bellamy *et al.* (1996a) found similar results for woodland islands in Cambridgeshire and Lincolnshire, and they have also been obtained for bird species numbers in habitat patches in other parts of the world (e.g. Kitchener *et al.* 1982; Howe 1984; Freemark & Merriam 1986; Møller 1987; Díaz *et al.* 1998).

Teasing apart the relative influences of area and habitat diversity on bird richness is always likely to be difficult. The problem is that area and habitat number are themselves often highly correlated (Harner & Harper 1976; Reed 1981; Rafe *et al.* 1985; Ford 1987; Rosenzweig 1995). Even if the species–area relationship were entirely a consequence of habitat number, the effect of area may be stronger in analyses because area can more easily be accurately assessed: there are many ways in which habitat number can be quantified, and there is no guarantee that the method chosen will reflect heterogeneity in those features of the habitat that influence bird richness (see, for example, Knight & Morris 1996). Given this problem, the analyses reported above are strongly suggestive of an effect of habitat, albeit not conclusive.

The way around the problem of covariation between habitat diversity and area is to examine variation in the number of species when one or other variable is constant: changes in area unaccompanied by changes in habitat diversity should lead to no species–area relationship, or alternatively, differences in habitat diversity in areas of similar size should be associated with differences in species richness. If habitat complexity is used as an indicator of habitat diversity, then there is significant evidence for a positive relationship with avian diversity (e.g. MacArthur & MacArthur 1961; MacArthur *et al.* 1962, 1966; Karr 1968; Recher 1969; Karr & Roth 1971; Moss 1978; Fuller 1982; Tellería *et al.* 1992). Rosenzweig (1995) uses data in Boström and Nilsson (1983) to show that area and avian diversity are unrelated on Swedish peat bogs once the effect of sample size has been removed, arguing that these represent a constant habitat. However, the extent to which that is true is unclear, as Boström and Nilsson themselves argue that variations in species densities are attributable to habitat variation between bogs. Nevertheless, no British birder intent on seeing a large number of species would prefer to spend the day in a square kilometre patch of deciduous woodland rather than a square kilometre containing deciduous woodland, grassland, open fresh water, fen and coastline. The same applies the world over. In sum, habitat diversity seems likely to be a major determinant of the species–area relationship.

Although there is an important role for habitat diversity in determining the number of species found in an area, this seems unlikely to be the sole effect. In