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## Species accumulation and species area curves — a comment on Scheiner (2003)

In his paper on species-area curves, Scheiner (2003) hopes to open a discussion on the biological and statistical underpinnings of species-area curves. Here we present views from studies undertaken in a very different domain: the marine environment. Scheiner presented a rather botanocentric view of species-area curves, where the sampling schemes are not at all like those used in marine subtidal habitats, which are the largest habitats on earth (Gray, 2002). Scheiner (2003) based his analysis on the quadrat approach to sampling where, of his four types of species-area curves, Types I and II were based on sampling using nested or contiguous quadrats, while the Type III curve was based on quadrats sampled in a regular but not contiguous grid

and the Type IV curves were from islands of varying sizes. When sampling the marine soft sediment habitat below diveable depths (c. 30 m for practical purposes) one has to sample using a grab or corer on a wire over the side of the ship. Nested, contiguous and regular sampling designs are simply not possible. Thus, most of our data (and we suggest probably most types of ecological data) are not obtained using the sampling protocols outlined by Scheiner. Yet the types of species-accumulation curves we obtain from marine data are the three basic types shown in Scheiner's (2003) Fig. 2. These are, on arithmetic scales (i) a stepped plot, (ii) a smooth curve rising steeply at first and then flattening out but not reaching an asymptote, and (iii) a linear plot of log species against log area. Thus, the sampling strategies that generate these curves can be from transects and from random samples within a given area or areas. Our experience, from a radically different sampling design to Scheiner's, leads us to rather different conclusions concerning the species-area relationship.

We believe that there is a fundamental distinction between species-accumulation curves and species-area curves. Sample-based species-accumulation curves are plotted from samples taken randomly within a given area (Gotelli & Colwell, 2001; Magurran, 2003), and take into account the number of species and their identity, but no information concerning the distribution of individuals among species is utilized. The order that samples are added to the species-accumulation curve affects the shape of the curve produced. This variation in the shape of the curve results from sampling error and heterogeneity among the species in the samples (Colwell & Coddington, 1994). If samples are taken along a transect and plotted as number of species accumulated against the accumulated area sampled, then one obtains a stepped curve (Scheiner's Type I). However, if one randomizes all the samples and then plots the same data, a smooth species-accumulation curve results (Scheiner's Type II). A variety of randomization procedures have been produced (Colwell & Coddington, 1994; Gray *et al.*, 1997) and recently Ugland *et al.* (2003) have devised an analytical procedure for deriving such curves. Figure 1 illustrates the two types of curves for a very large marine data set of the fauna of soft sediments sampled by taking five randomly taken grabs (the sampling units), over five areas along the Norwegian continental shelf (Ellingsen & Gray, 2002). The important point that we make is that these two curves are for the same extremely large data set and show how species

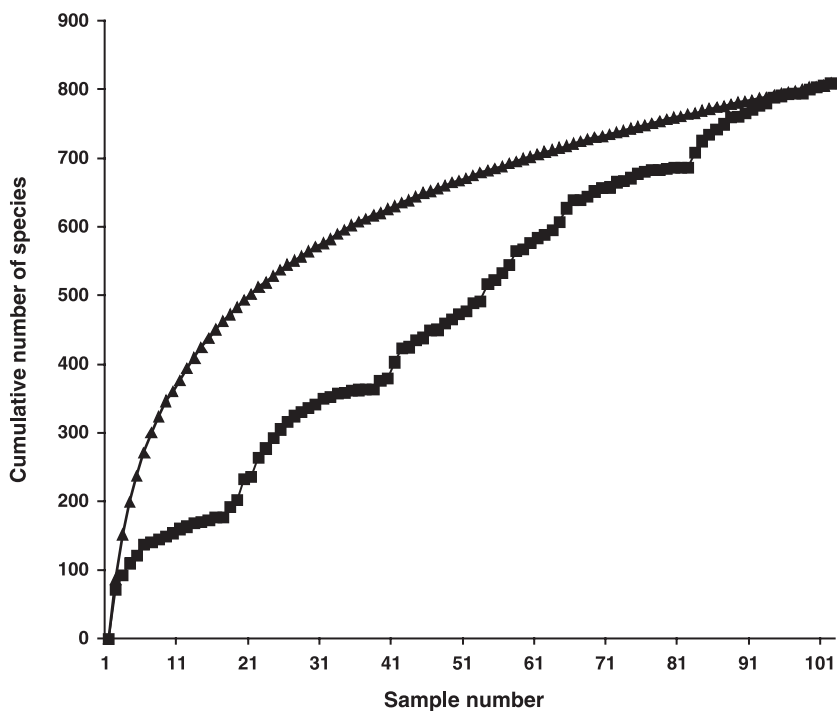
accumulate as sample size is increased. The species-accumulation curves can be derived for samples, areas or, as here, the whole Norwegian continental shelf. The shape of the species-accumulation curve is semilogarithmic (Ugland *et al.*, 2003) and the shape does not vary with the size of the area sampled. Species-accumulation curves measure the rate of accumulation of different species as the area sampled is increased.

An important aspect is that the data shown in Fig. 1 are based on samples taken at random within five separate areas along the Norwegian continental shelf. We believe that the production of a smooth semilogarithmic curve as shown in Fig. 1 (and Scheiner's Fig. 2b) is not the result of the sampling scheme as claimed by Scheiner (p441), but rather constitutes a general pattern of species-accumulation in randomized samples.

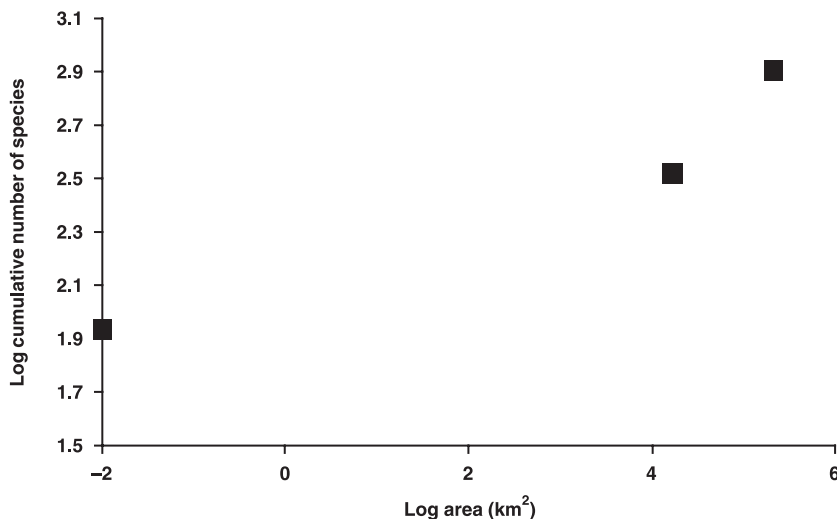
We believe that the species-area curve measures something quite different, namely how the number of species varies with the size of area sampled. When Arrhenius (1921) first derived his log-log species-area relationship he studied non-native plant species on islands of varying sizes, primarily from the Stockholm archipelago, Sweden. What he measured was simply the number of species on each island, where the islands were of different sizes. The species present on the largest island may have included all of the species on the smaller islands or none of them. Thus the species-area plot measures the relationship between number of species and area over a range of scales from fine to coarse. Figure 2 shows data for the benthos of the Norwegian continental shelf measured over the three scales, sample, large area and whole shelf. The species-area relationship is roughly linear in log-log space, as is usually found (Rosenzweig, 1995). In order to clarify this point we use a simple example. Suppose that there are 5 islands of sizes 1, 2, 4, 8, 16 that are sampled in proportion to their size, i.e. the number of samples are, respectively: 2, 4, 8, 16, 32 and the total number of samples is 62. The number of species on the islands follows Arrhenius's Law with  $z = 0.30$ : 10, 12, 15, 19, 23. All replicates within each island are identical. Consider two alternative structures:

**1 Archipelago 1:** 10 species are common to all islands, and all species found in one island will be found in all the larger ones (i.e. the data are perfectly nested). The numbers of species in these five islands are therefore, respectively, 10, 12, 15, 19 and 23, so in total there are 23 species distributed over these islands.

**2 Archipelago 2:** No species occur in more than one island (all are endemic). The total



**Figure 1** Species-accumulation curves for the benthic fauna of the Norwegian continental shelf (from Ellingsen & Gray, 2002). The stepped curve (Scheiner's Type I) is for data treated as a single transect from the furthest South sample to the furthest North sample. The smooth semilog curve is for the randomised samples using Colwell's EstimateS program (Colwell, 1997).



**Figure 2** The species-area curve for data for the benthos of the Norwegian continental shelf for three sampling scales, being those of: samples, areas, and the whole shelf. See Ellingsen & Gray (2002) and Ugland *et al.* (2003) for details of the sampling design and areas involved.

number of species on each island is still 10, 12, 15, 19 and 23, but since no species occupies two islands simultaneously, the total number of species in this archipelago is now  $10 + 12 + 15 + 19 + 23 = 79$ .

Figure 3 shows that there is only one species-area curve for both Archipelagos. However, the corresponding nested curves (Scheiner Type I) and species accumulation curves (Scheiner Type II or Type III) are widely different for the two archipelagos (Fig. 4). Clearly, the species-area curve should not be confused with the species-accumulation curves. From Figs 3 and 4 it can be seen that there are in fact only three types of curves, not

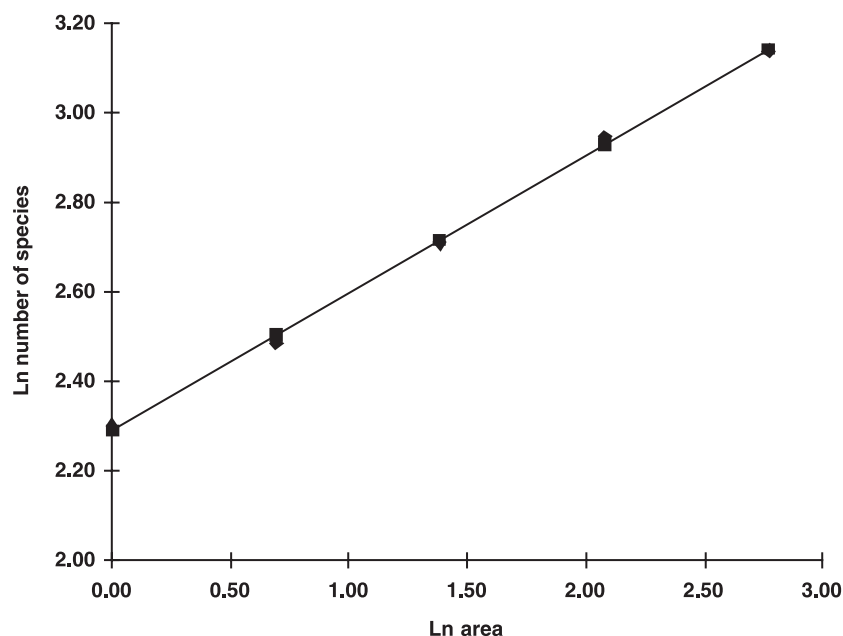
six. These are the nested curve (Scheiner Type I), the randomised curve (semilog; Scheiner Type II and III) and the species-area curve (log-log).

Yet, if one takes only extremely small samples and increases the area sampled, then what one primarily will be measuring is species accumulation. There are many examples of ecological surveys sampling small areas only and calling this a species-area study. For example McGuinness (1984) studied species numbers on boulders of different size, ranging from only  $30 \text{ cm}^2$ – $2000 \text{ cm}^2$  in the rocky intertidal. Unsurprisingly, he found typical semilogarithmic curves.

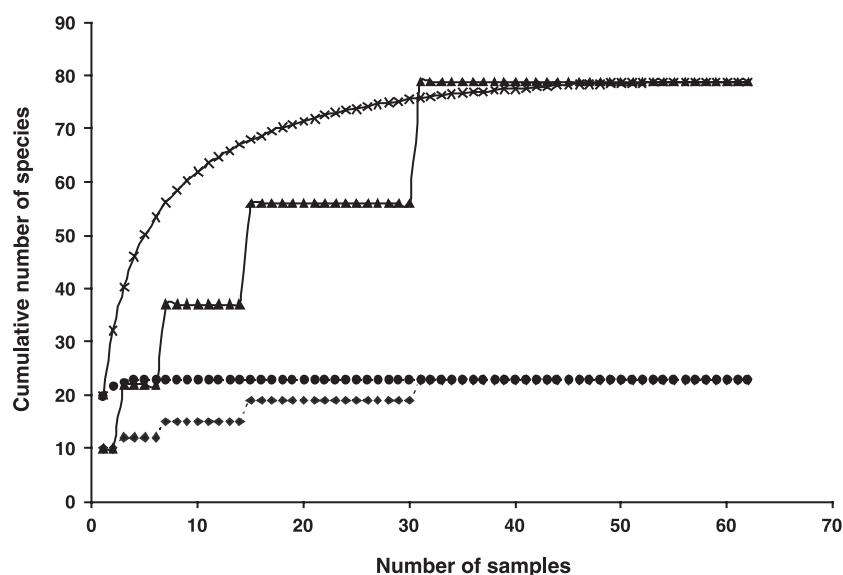
The ecological questions that relate to the two relationships are also different. Species-accumulation curves are used to try to ascertain how many species occur in a given area. Species-area curves are used to ask more fundamental questions relating to macroecological patterns (*sensu* Brown, 1995; Rosenzweig, 1995; Gaston & Blackburn, 2000) as initiated by MacArthur (1965). We believe that the distinction between species-area and species-accumulation curves is extremely important.

Scheiner (2003) discusses the two major components of diversity: inventory diversity and differentiation diversity (Whittaker, 1972). Whittaker (1972) recognized that species

**Figure 3** Species-area curve (Ln number of species against Ln area) for two artificial archipelagos containing 5 islands of different sizes and the same number of species on each island. Linear regression  $Y = 0.3066x + 2.29$   $R^2 = 0.998$ . Squares Archipelago 1, diamonds Archipelago 2.



**Figure 4** Species accumulation curves for the two artificial archipelagos described in the text. The lower two curves are for Archipelago 1, showing stepped accumulation (Scheiner Type I) and analytical species-accumulation curves (Scheiner Type II or III). The upper two curves are for Archipelago 2, showing stepped accumulation (Scheiner Type I) and analytical species-accumulation curves (Scheiner Type II or III).



richness (and diversity) could be measured over different scales. Inventory richness has been simplified to that of a sampling unit (point richness), of a sample (alpha richness), of a large area (often called a landscape or region — gamma richness) and the biogeographical province (epsilon richness) (Whittaker, 1972; Gray, 2000; Magurran, 2003). The units of inventory richness are number of species. Differentiation richness measures a quite different aspect, namely the similarity between the species composition at the different scales sampled, or the turnover of species along a gradient (Whittaker, 1972) and is called beta diversity. [An interesting point to

note is that the distinction between inventory richness and differentiation richness is closely similar to that between species-area curves and species-accumulation curves; with inventory richness one simply uses the number of species, whereas with differentiation you compare the differences in species composition].

Beta diversity compares the number of species (or the similarity in species composition) between gamma and alpha richness or epsilon and gamma richness. [There are differences of opinion as to whether this should be measured as a ratio as Whittaker (1972) suggested or as a difference (Loreau, 2000)]. Beta diversity is not the slope of the species-accumulation

curve as claimed by Scheiner (2003). [Scheiner (2003) refers to MacArthur (1965) as his reference to beta being the slope of the accumulation curve, but we can find no reference to such a relationship in MacArthur's paper]. Whittaker (1972) discussed the slope of the species-accumulation curve (p222) as a measure of alpha diversity, not beta. He stated that this measure of alpha diversity 'is thus transformed from numbers of species per sample to a rate,  $d$ , at which species are added with expansion of the sample.' As Magurran (2003) and Koleff *et al.* (2003) show, there are many methods of measuring beta diversity (28 in Koleff *et al.*, 2003) and the slope of the

species-accumulation curve is not among them. We believe that the general consensus among ecologists is that beta diversity is a measure of the change in species composition along a gradient, rather than the slope of the species-accumulation curve, as claimed by Scheiner (2003).

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