

Species–area relationships at small scales in continuum vegetation

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Species–area relationships (SARs) are well known to be variable, particularly at the left hand end, i.e. at small areas with low numbers of species (Williamson *et al.* 2002). Here I show that some of this variability is a consequence of the way that species are recorded. The relationship is, here, always presented in a standard way, i.e. on logarithmic axes, of log species vs. log area. The axes are in homogeneous measure, making statements about slopes simpler. The slopes will be referred to, again in the standard way, as z .

Theory

First consider a diagrammatic, theoretical, type of vegetation which I will call continuum vegetation. By this I mean vegetation that has absolutely continuous cover but only one individual at any one point: each individual has a finite area and, viewed from above, the ground is everywhere obscured by vegetation. Continuum vegetation is a theoretical concept but is approximated by some real types of vegetation, most notably perhaps by the closed canopy of a tropical rain forest. Data from such a forest, as well as data from a temperate study, are used below to illustrate the theoretical points that will be developed. The former communities are the basis of Hubbell's famous 'Neutral theory' (Hubbell 2001), and he refers to them (pp. 51 ff.) as 'space-limited communities', 'biotically saturated with individuals', leading to the theorem 'the dynamics of [such] ecological communities are a zero sum game'. As he points out, continuum structure is commonly found in many other sorts of vegetation and is not universally found in tropical rain forests. It is also found in some animal communities such as coral reefs. This mathematical structure is exactly that found in geological maps, where only the surface geological type is shown at any point; Williamson (1981; fig. 5.14) derived an analogue of a species–area relationship from such a map. Although in real vegetation there are usually some gaps and some overlap of individuals, Hubbell argues that such deviations are often negligible while the zero sum dynamics have far reaching consequences.

When recording the presence or absence of a species more than one convention is possible. One, the any-part

system, used for instance by Crawley & Hurrell (2001) in the temperate example considered below, records a species as present if any above ground part of an individual is in the sample area. They recorded all species of vascular plant of whatever size. Using a quadrat and looking at it vertically, the question is can any part of a leaf or stem of a species be seen in the quadrat? If so, the species is recorded as present. (I know of no study attempting to record underground parts, which is not surprising, although they are important parts of plants.) Another, the grid-point system, used in the network of permanent forest sites of the Center for Tropical Forest Science of the Smithsonian Tropical Research Institute (Condit 1998; Burslem *et al.* 2001), records each individual as a point with exact coordinates on a grid (Condit *et al.* 1996; Condit 1998). In that survey, a point representing the centre of the trunk of each tree over 1 cm d.b.h. is recorded on a plan in the field and the position digitized later. A sapling a few cm from the buttress of a large tree may consequently appear in the records to be several metres from the tree (R. Condit pers. comm.). There are obvious merits in both systems but here I am merely concerned with their effect on the shape of SARs.

In the any-part system with continuum vegetation, no matter how small the quadrat or other sampling device at least one species will always be present. That follows from the definition of continuum vegetation. Consequently the SAR will become horizontal at the left (with the usual convention of area along the abscissa with small values to the left), going to an asymptote at one species. (The absence of an asymptote suggested in the titles of Williamson *et al.* (2001, 2002) refers only to that at the right side, i.e. at large areas.) So the SAR in the any-part system goes asymptotically to a slope of zero at very small areas.

What happens with the grid-point system in continuum vegetation is somewhat more subtle. Consider a square quadrat in which only one individual of one species has been recorded, a quadrat with but a single tree. If the quadrat is now divided into four squares, then, because of the point recording, only one of these subquadrats will contain the tree record, the other three will be empty. (Points on an edge are scored as in only one quadrat.) The average species density in the quarter areas will be a quarter of a species. Similarly for any finer division, a $1/n$ area will have a $1/n$ species density and the SAR for these divisions will have a slope of

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exactly one at the left hand side. This argument was first put forward by Plotkin & Levin (2001), although without the extensions, the new arguments, in the next two paragraphs or the conclusions reached in this paper.

Consider next a quadrat with many trees but only one individual of any one species; the number of species equals the number of trees. Then the argument in the previous paragraph holds for each species and so for the set as a whole. If there are s species in the whole quadrat, there will be s/n on average in any $1/n$ subsample. This more realistic community will also have a SAR with a slope of one.

It might be thought that those arguments would lead to an effect only at very small quadrats, when all species have not more than one individual in any quadrat. Because of averaging, that is not so. An effect, less strong, will be found at all quadrat sizes within a large area in which all the possible quadrats are averaged. The effect of averaging is that all the species in the whole area contribute, either as units or, more commonly, as a fraction of a unit, to the average at every subarea. To take a simple case, if there is only one individual of a species, species H say, in the whole area, it will be recorded at one point in that area and will contribute one, a unit, to the count of species. In the two halves of the area, the recorded point will be either in one half or the other, giving a unit in one half, a zero in the other half, so the contribution of species H to the species average at the half area is half a species. As the area is further subdivided, its contribution to the species average will always be $1/n$ of a species for $1/n$ of the whole area. This effect will happen for all species from the quadrat size where there is not more than one individual of a species at that quadrat size in the whole area. The argument is the same as the argument above, with the additional consideration that the average includes contributions from all species. Each species will start to contribute at a rate given by the slope of unity once that species has not more than one individual in a quadrat. As the quadrats get smaller, more and more species will so contribute. The effect is that the SAR will gradually approach a slope of one. The approach starts at the largest quadrat size in which at least one species is represented by only one individual per quadrat and is complete when all species reach that state. That start will normally be from the largest area averaged. It is important to note that this effect is an inevitable consequence of combining point recording with averaging. The grid-point system will produce a species–area relationship which goes asymptotically to a slope of one at small areas.

The two recording methods are both natural conventions and easily justified. Nevertheless, at the extreme left hand side of the SAR, in continuum vegetation, one (the any-part system) goes to a slope of zero, the other (the grid-point system) goes to a slope of one, the two natural limits for all SARs (Williamson 1988). All this is true for theoretical vegetation. What happens in practice?

Practice

The studies by Crawley & Harral (2001) and the tropical forest data of Plotkin *et al.* (2000) are notable for the number of quadrats recorded and for the range of areas studied, requiring exceptional skill and effort. They more than suffice to show that the effects discussed above are realized in practice. The results from these surveys are shown as conventional (Arrhenius) log-species vs. log-area plots in Fig. 1 and as the local slopes of the Arrhenius plot (labelled z , the usual convention) vs. log-area in Fig. 2. Each study illustrates one point in the theory. The comparison of the studies is primarily with the theory rather than with each other.

Crawley & Harral (2001) used the any-part system to record all vascular plant species of any size from small quadrats in Silwood Park (the location of their campus) through larger quadrats in Berkshire (the county containing Silwood Park) to the whole of Britain. They recorded from all habitats in Silwood Park, but, at the smallest scales, only the data for their four approximations to continuum vegetation, namely woodland, grassland, bracken and heath, are used here. These four types are shown separately in Fig. 2 but averaged in

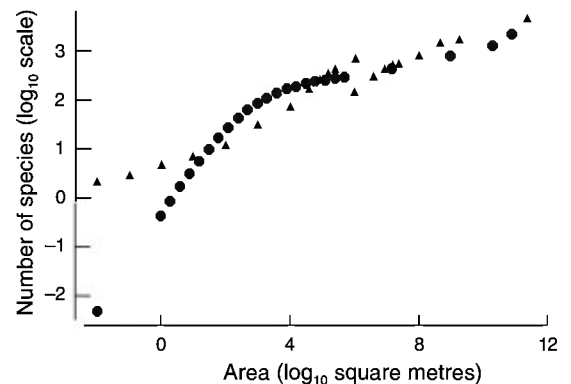


Fig. 1 Species–area relationships in Panama (●) and Britain (▲). Data from Crawley & Harral (2001), Hubbell (2001) and Plotkin *et al.* (2000). Note the logarithmic scale on both axes.

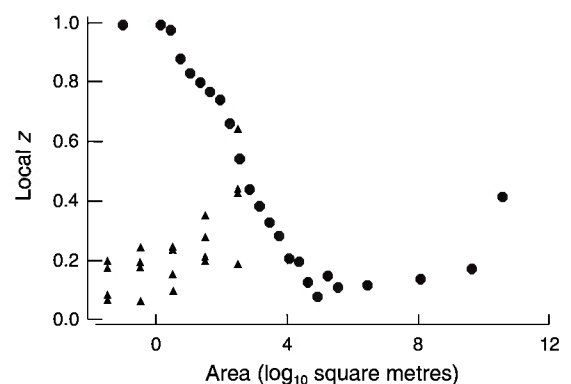


Fig. 2 Slopes of the species–area relationship in Panama and Britain plotted against the logarithm of the area. Symbols and data sources as in Fig. 1. The slope, z , is calculated between successive points on Fig. 1.

Fig. 1, whereas, at larger scales, the averages given in their tables are used: Fig. 1 therefore shows data from a wider range of temperate areas than Fig. 2.

Plotkin *et al.* (2000) used grid-point system censuses of 50-ha plots in five tropical forests. All gave the same pattern and only data from the forest on Barro Colorado Island in Lake Gatun in the Panama Canal are considered here. The tropical data in Figs 1 and 2 from one metre square (actually a touch less because of binary division) to 50 hectares are taken from the graph in Plotkin *et al.* (2000); the points to the right of that from a graph in Hubbell (2001) which gives data from the whole of Barro Colorado Island, the one-time Panama Canal Zone, Central Panama and the whole of the Republic of Panama.

The point at the extreme left of the tropical forest plots in both figures is not taken directly from the data in Plotkin *et al.* (2000). I have been able to calculate this using some particular features of the grid-point system used by the Center for Tropical Forest Science. Each 50-ha plot (1×0.5 km) is gridded. For each 5×5 m subplot, the survey team delineates the four edges and the two diagonals. The estimated centre of each tree of ≥ 1 cm d.b.h. is marked on a diagram and later digitized to the nearest 10 cm (Condit 1998). This procedure in effect grids the 50-ha plot into 50 million squares of 10×10 cm. No two trees have the same 10 cm coordinates (He & Gaston 2000) and each square therefore has either one or zero individuals and so one or zero species. (Individuals falling on an edge get recorded in one such small quadrat.) The total number of individuals, given for each of five 50-ha plots by Plotkin *et al.* (2000), gives the occupancy of these small squares and so the average species number per small square. It can be seen in Fig. 1 that this extra point fits beautifully on the data published by Plotkin *et al.* (2000). It can also be seen that 10×10 cm is, by coincidence, also the smallest size quadrat used by Crawley & Harral (2001) although, of course, the scale of the vegetation is distinctly different in the two studies. If a forest is an area covered with vegetation and a desert is an area with almost none, then this data base forest is a desert; 99.5% of it is empty, only 235 317 quadrats out of 50 million are occupied.

In Fig. 1, it is clear that the average slope across all the British points and across the right hand points in Panama is fairly standard at 0.15–0.3. Both Hubbell (2001) and Crawley & Harral (2001) emphasize the variation in the slope at different scales, which is true, but the general linearity of the plots is still striking. Perhaps this is the point to reiterate the sometimes misquoted result in Williamson (1988) which came from a survey of surveys. Somewhat more than half (i.e. most) of the published slopes of SARs are between 0.15 and 0.4. The median slope is somewhere between 0.25 and 0.3 but many individual slopes are not only outside that range but vary all the way between the theoretical limits of 0.0 and 1.0. It is also clear from Williamson (1988), e.g. in his fig. 4.2, that slopes from an individual very

small area to a very large one will almost never be constant even though sets of independent areas do often (although only up to 75% of the time) give satisfactory linear log-log plots (Williamson 1988; Williamson *et al.* 2001).

The most marked deviation from linearity in Fig. 1 is seen amongst the points from the 50-ha plot. These appear to be going rapidly, with decreasing area, to a slope of one, as predicted above. The British points appear to be going, more slowly, to the predicted slope of zero. Both points are more easily studied in the plots of slopes (z) against area in Fig. 2. The considerable scatter and visible trend in the British data are evident but the approach to zero is slow. The area differences for the British points in Fig. 2 are times 10. The smallest area plotted is 316 cm^2 , the geometric mean of 100 cm^2 and 1000 cm^2 . It would seem the slopes are unlikely to reach zero before at least another couple of 10-fold shifts to the left, around perhaps 1 cm^2 . But the effect seems to go up to the maximum area, 1000 m^2 or 0.1 ha, for which Crawley & Harral (2001) give data for all four communities.

The variation in z in Panama is much more striking. Figure 2 is a straightforward transformation of fig. 2(b) in Plotkin *et al.* (2000) but with the addition of the extreme left hand point, mentioned above, and four to the right (from Hubbell 2001). The slope from the 50-ha plot to Central Panama is reasonably constant at about 0.15. The slope in the three smallest zones (0.01 m^2 – 1 m^2 , 1 – 2 m^2 , 2 – 4 m^2) is effectively one, as predicted. The transition is monotonic from 3 ha downwards.

From the number of individuals in each of the different species in the 50-ha plot (Hubbell 2001; fig. 3.4) it would be possible to calculate the progression to a slope of unity on the assumption that all species are absolutely regularly distributed. The binary scale in that Hubbell figure neatly matches the binary divisions of area used in Figs 1 and 2 here. From the argument above, the 21 species with but a single individual will affect the slope between 50 ha and 25 ha. The 18 species with two individuals will affect the slope between 25 ha and 12.5 ha. Continuing that way, all species, if uniformly distributed, would affect the slope from 16 m^2 to 8 m^2 . Most species are in fact aggregated (Condit *et al.* 2000), so the empirical figure of 4 – 2 m^2 at which a slope of unity is found agrees quite well with the theory.

Conclusion

Depending on the method of recording plants in continuum vegetation, the species–area relationship can flatten out to the minimum possible or steepen to the maximum possible for such a relationship. The differences are consequences of the recording systems and have nothing to do with biology or environmental variation. The effect, judged by the limited data here, is much milder with the any-part system of recording

than the grid-point system. It is possible that some intermediate method should be preferred but I know of no data to test that and the criterion to use is not obvious. Until that is clarified, it would seem safest to use the any-part system before attempting biological or environmental interpretations. Many papers on SARs do not describe the sampling methods used. Yet when comparing SARs from different studies, or when comparing them with theory, it is important to ensure that sampling effects do not vitiate the comparison. If the sampling methods are uncertain, the comparison will be too.

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