Spatial variation in power-law species-area curves for a single clade in a single biome. PROPOSED CONFLATION, POSSIBLY FOR ECOLOGY BUT NOT SO FORMATTED. ALL PREVIOUS COMMENTS SUPPRESSED.

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A note on conventions: this paper contains comments not meant to form part of the submitted text, formatted as follows:

[HL: MATTER IN CAPITAL LETTERS, USUALLY PRECEDED BY HL: AND USUALLY ENCLOSED IN SQUARE BRACKETS ARE COMMENTS BY HENRI]

To do list:

– Grayscale maps (7 of them in figs 10–12; 10(c) and 12(c) already exist)

– Last-minute literature references

– Decide on journal, format appropriately, submit

Abstract

We present and discuss data demonstrating large within-region variability of the parameters of the Arrhenius species-area formula. We limit ourselves to one vegetation type, namely the entire Fynbos of the Cape Floristic Region, South Africa. We consider only one clade, namely Proteaceae, which is almost entirely endemic to Fynbos. We use over 250 000 records. We include 10 levels of spatial resolution. At the finest level, this consists of almost 10 000 $1' \times 1'$ cells, all of which contain at least one record. We show that Arrhenius species-area parameters vary widely across locations when scale is kept constant and across scales when location is kept constant. We show that the parameters are correlated, and that moreover the spatial variation of the residual of this correlation has spatial structure.

Keywords: species-area curve, spatial variation, species richness, Protea Atlas, Fynbos, Proteaceaee, Cape Floristic Region

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Introduction

Species-area curves are widely considered to be of fundamental ecological significance (Rosenzweig 1995; Lomolino 2001; Ney-Nifle and Mangel 2000; Driver et al. 2003). This significance is typically interpreted as follows: the parameters of a species-area curve fitted to data from some coherent ecological entity are a property of that entity. In that sense, a simple curve summarises the spatial pattern of species richness. In particular, one should be able to predict species richness simply from area, which would be very useful in conservation management (Driver et al. 2003). The area in question may vary from small ($< 10^2$ km^2) to large ($> 10^6$ km^2), spanning the range from landscapes to continents.

We report here that detailed analysis of fine-grained data on species occurence does not support such an ambitious interpretation.

We studied at a large data set for the distribution of all Proteaceae that occur in the entire Cape Floristic Region (CFR henceforth), using the Arrhenius formula $N = cA^z$, where N is the number of species and A is the area. We expect other two-parameter functions to give similar results (see the Discussion section; see Connor and McCoy (1979) and Matter et al. (2002) for other possible formulae). If the curve were a property of the entire area, applicable to all sub-areas inside it, then any representative set of data pairs (A_i, N_i) should yield satisfactory estimates of the parameters c and z. We report here that this is not the case; instead, the estimates depend strongly on how the data pairs (A_i, N_i) are selected.

This leads to following questions: how variable are the estimates for c and z, are these estimates correlated, and do these estimates show any spatial signal? The answers are: extremely variable, strongly correlated, and with some spatial signal that we indicate but do not fully analyse. Additionally, we are able to distinguish variability between locations from variability between scales.

Methods

Our data come from the Protea Atlas Project (**http://protea.worldonline.co.za**) records of Proteaceae. The basic Protea Atlas site record sheet gives a census of all species of Proteaceae present in a centrally geo-referenced area of uniform habitat up to 500 m in diameter (Rebelo 1991). Data were collected by professionals and by amateurs under professional supervision. We limited ourselves to the Fynbos biome (Cowling 1992) which is endemic to the Cape Floristic Region, the smallest of the worlds six floristic regions (Takhtajan

1986). Thus our study concerns all species of a clade occuring in all of one vegetation type endemic to an entire biome. Moreover, the species in this study are all endemic to Fynbos. Our final data set contained 252 513 records of 374 species at 61 591 record localities.

The analyses below were based on counts constructed as follows. We started with a raster of $1' \times 1'$ cells (roughly 40 000 of them). From this we amalgamated adjacent cells to obtain larger units of sizes $3' \times 3'$, $7' \times 7'$, $15' \times 15'$, $31' \times 31'$, $63' \times 63'$, $127' \times 127'$, $255' \times 255'$, $511' \times 511'$ and $1023' \times 1023'$. Thus this study is at ten levels of focus, in the sense of Scheiner et al. (2000). The larger units overlap to some extent. Each of the larger units was centred on a $1' \times 1'$ cell, called its "focal cell" henceforth. Every focal cell is at the centre of a full sequence of associated larger units. These are similar to the nested sequences used in Koleff and Gaston (2002), where the units are termed "tetrads".

For the purposes of this study, a cell was regarded as a Fynbos cell if it contained a Protea Atlas record, which is acceptable at these scales. Our database contains 9 426 Fynbos cells for the entire CFR and 10 463 cells for the sub-regions (the apparent anomaly is explained below).

We counted the number N of Proteaceae species present in each unit. We also found the area A occupied by Fynbos in a unit as the count of Fynbos cells in that unit. At the largest scale, each one of the $1023' \times 1023'$ units contains all of the Fynbos cells.

For each of the estimates below, we assembled an appropriate data series of the form (A_i, N_i). Upon taking logarithms, the Arrhenius equation becomes $\log(N) = \log(c) + z \log(A)$. We obtained estimates of intercept $\log(c)$ and slope z by least-squares fits to $(\log(A_i), \log(N_i))$. We used the following software packages: ARC-GIS, ARC-INFO, ARC-MAP, MS-Excel, gnumeric and GNU Octave.

The Cape Floristic Region has been divided into several sub-regions in the past. Here we use sub-regions based on centres of endemism for the Proteaceae (modified from Cowling, Holmes, and Rebelo 1992) (see Figure 1). All but two of the sub-regions are simply connected and also contiguous with another, so that they form a simply connected whole. However, the Karoo and Swartberg Islands subregions each comprise several isolated pockets of Fynbos within other vegetation types.

[Figure 1 about here.]

For each sub-region, we classified a cell as in the sub-region if more than 50% of the cell's area falls in the sub-region. This was done using the GIS packages, and led to approximately 10% of the cells being counted in more

than one sub-region, hence the anomaly between the overall count and the sum of sub-regional counts.

Samples that vary by location and by scale

When all units of all sizes are considered, one gets a data set with approximately 100 000 $(A_i,\ N_i)$ pairs. This set gives a single estimate of the intercept $\log(c)$ and slope z of the Arrhenius line in log-log space.

We also constructed for each sub-region a data set from the counts of all units of all sizes in that sub-region. This gives 29 estimates of the Arrhenius parameters, one for each sub-region.

The subregions themselves were also considered as areal units. This yields a shorter data set, of 29 $(A_i,\ N_i)$ pairs, where each A_i is the number of fynbos cells of a subregion and N_i the corresponding species count. Again, only one estimate of parameters come from this data set.

Samples that vary by location but not by scale

Consider all units of a given size, for example $7' \times 7'$. It is obvious that they will vary in the number of species they contain. However, at all sizes except $1' \times 1'$ and $1023' \times 1023'$, they also contain different amounts of Fynbos cells. So by using all units of a given size, we may construct data sets where the counts vary by location but not by scale. "Scale" in this sense is very similar to "focus" Scheiner et al. (2000).

We did this for the entire CFR, which gave 8 single-scale estimates of the parameters $\log(c)$ and slope z.

We repeated this for each sub-region. The results were similar, and we do not report them here.

Samples that vary by scale by not by location

For each focal cell, we considered the 10 units centred on that cell (for a similar nested sampling method, see Preston 1960 and Rosenzweig 1995). Since the units in such a sample have a common centre but different sizes, they vary by scale but not location.

For the whole CFR, these data sets yielded 9426 pairs of Arrhenius parameters, one for each $1' \times 1'$ cell. We refer to this as the "nested series, full CFR" parameter estimates.

For sub-regions, each nested series was terminated at the first unit in which the entire sub-region was contained (of course cells from outside the sub-region were ignored). Locations in different sub-regions have different sample sizes,

determined by the unit area encompassing the entire sub-region; the largest unit varied from $15' \times 15'$ to $511' \times 511'$. We refer to parameter estimates from these data sets as "nested series, sub-regional" values.

Thus each of the Fynbos cells in the CFR yielded two curves: one for the entire CFR and one for its sub-region and correspondingly two pairs of Arrhenius parameters. Because each estimate has a geographic reference, namely the central cell, maps of a given parameter (may) reveal spatial variation.

For each sub-region we constructed a nested series with that sub-region at its centre. Adjacent subregions were added until the full CFR was reached. This yielded 29 estimates of Arrhenius parameter pairs, each of them spatially referenced to a particular sub-region. [HL: I WOULD LIKE TO SEE A MAP OF THESE RESULTS.]

Results

Variation across location and scale

The species-area relationships across all units in the entire CFR is shown as pair of scatter-plots in Figure 2. The Arrhenius parameters are $\log(c) \approx 0.64$ and $z \approx 0.47$. The latter value is rather high compared to traditionally expected values (Rosenzweig 1995; Preston 1960) and reported values (Cowling et al. 1992; Driver et al. 2003; Procheş et al. 2004).

[Figure 2 about here.]

Subregional data are exemplified by the four scatterplots in Figure 3. The 29 estimated parameter values for all cells at all relevant focus levels (i.e. the largest scale is the smallest at which the entire region is included for every focal cell) for each subregion are given in Table 1.

[Figure 3 about here.]

[Table 1 about here.]

Across the subregions, the estimates are $\log(c) = 0.40$ and $z = 0.50$ (see Figure 4)

[Figure 4 about here.]

Variation by location but not by scale

At a single focus, the estimates for the Arrhenius slopes are far higher than over the entire data set (Figure 2). Single-focus slopes (z) show a decrease from 1.22 ($3' \times 3'$) to 0.88 ($31' \times 31'$) over smaller scales, but then increase to

1.25 ($127' \times 127'$) and decrease to 1.08 ($511' \times 511'$) at the largest relevant focus level. Note that $63' \times 63'$ to $127' \times 127'$ are the focus levels that correspond best to the area of the sub-regions, so that the increase over intermediate scales might be a sub-regional effect.

Intercept ($\log(c)$) is positive only for the smallest focus level (the estimate at $3' \times 3'$ is about 1.4 species per cell). It goes down to $\log(c) = -2.05$ at $127' \times 127'$, which is about 0.006 species per cell, and then increases slightly. These unrealistic values are explained as follows. At the larger scales, none of the units contain only one cell. Estimates of $\log(c)$ at these levels are extrapolations beyond the data, and there is no reason to expect them to be realistic. In contrast, the overall estimate of $\log(c) \approx 0.64$ of the previous section gives around 4 species per $1' \times 1'$ cell. This matches the data, which gives a mean of 6.86 species per cell, with a standard deviation of 5.09.

[HL: TONY, WHAT FOLLOWS IS YOUR STUFF. NOT SURE I'VE CAPTURED YOUR IDEAS AT ALL ADEQUATELY; OF COURSE THIS PARA AND THE PRECEDING DON'T BOTH GO IN] Thus the sub-regional data under-estimate the species richness at infra-sub-regional scales. By contrast, the closest unit size is $127' \times 127'$, as the sub-regions vary between 10–90 cells high by 30–250 cells wide. At this scale (see above), $z = 1.25$ and $\log(c) = -2.05$, extrapolating to 0.01 species per cell. Thus sub-regional species area-curves (non-overlapping, defined by centres of endemism, n=29) yield far lower estimates than unit scale curves (overlapping, one per focal cell, n$\approx 10^4$).

At the larger scales, the units overlap substantially. The resultant correlation decreases the apparent variance in both $\log(A)$ and $\log(N)$. In principle, this could be corrected by calculating the effective sample size, but since no statistical inference was attempted in this paper, we did not do so.

Variation by scale but not by location

We now turn to nested data, where all the units in a given data set have a common centre but different scales. This gives a spatial reference to the resulting estimates of $\log(c)$ and z. Each data set contains at most 10 pairs, but there are very many of them. In fact, for each of the approximately 10 000 cells, there are two data sets and two pairs of Arrhenius parameters. We give the histograms of their values in Figure 5, which show that these estimates are more or less normally distributed.

The slope (z) has a modal value of 0.45 for the entire CFR, and 0.34 for the sub-regions. Similarly, the intercept ($\log(c)$) for focal cells (Figure 5) has a modal value of 0.8 for the entire CFR and 0.9 for the sub-regions. In both

cases, the scatter of values is much greater in the sub-regions than in the entire CFR ($\log(c)$: from -0.29 to 1.6 *vs* from -0.20 to 1.4; z: from 0.07 to .93 *vs* from 0.28 to 0.75).

[Figure 5 about here.]

Correlations between parameter values

It may perhaps be suspected that $\log(c)$ and z will be correlated (on the grounds, for example, that species richness and endemicity of regions are positively correlated). Nevertheless, the strength of the correlation and its variation by location and scale is of interest. We were able to find two cases of use: from the subregions, we get a set of 29 estimates of the Arrhenius parameters, and from the nested data we get three sets, two of approximately 10 000 pairs and one of 29 pairs. The single-focus data sets are inappropriate for regression analysis, since the estimates of $\log(c)$ are unreliable (see discussion above).

Parameter correlations when both scale and location vary in each data set

The Arrhenius parameters for each sub-region vary greatly (Table 1) but as Figure 6 shows, without much correlation between $\log(c)$ and z.

[Figure 6 about here.]

Parameter correlations when only scale varies in each data set

In the previous case, there were few parameter estimates we could use for a regression analysis. The nested data sets yield many more: two pairs for each focal cell, as well as one pair for each focal sub-region. Figures 7, 8 and 9 show that correlation is high among all three pairs of variables: z vs $\log(c)$, $\log(N)$ vs $\log(c)$ and $\log(N)$ vs z when estimated from nested data sets.

[Figure 7 about here.]

[Figure 8 about here.]

[Figure 9 about here.]

The data sets from series of nested around focal cells (Figures 7 and 8 show a similar pattern: when z and $\log(c)$ are correlated, the variability is approximately constant across the scatterplot, but when the regression includes $\log(N)$, the variability is low for high values and high for low values. It is also clear that for data sets truncated at sub-regional boundaries, the variability is higher. This is likely to be a statistical artefact, since the series are shorter on average.

On the other hand, the nesting of subregions (see Figure 9) yielded regressions with very small residuals. The slope of the regression line for z vs $\log(c)$ is also much steeper, at about -1 as against roughly -0.3. That is, using nested sub-regions rather than nested tetrads produces a much stronger correlation between slope and intercept.

Spatial Signal

[Figure 10 about here.]

[Figure 11 about here.]

[Figure 12 about here.]

The variation in the parameters of $N = cA^z$ are spatially non-random. This variation should be considered against the background pattern of species richness in the CFR, as seen in Figure10. Species richness is greatest (up to 39 Proteaceae species per $1' \times 1'$ grid cell) in the south west (Cape Peninsula, Hangklip: see Figure 1 for location and extent of sub-regions listed) of the CFR. Two streams of elevated richness spread from this nexus. One goes northwards (Hawequas, Groot Winterhoek, Cederberg) over a broad and largely mountainous area. The other goes eastwards mostly along three mountain range axes separated by valleys: coastal (Riviersonderend, Langeberg, Outeniqua), inland (Klein Swartberg, Swartberg) and southern (Agulhas, Potberg). In addition to the species-poor sub-regions, there are extensive areas of non-Fynbos (Proteaceae free) areas between these ranges, occupied by Renosterveld, Succulent Karoo, Afromontane Forest and Thicket vegetation (Rebelo 2004). Visually there is a strong spatial and magnitude correspondence between species richness and intercept $\log(c)$ (Figure 10b), although we did not run any statistical tests of the spatial patterns. The spatial distribution of the intercept ($\log(c)$) mirrors the species richness patterns, but smooths the data to some degree, with values of up to 1.436 (or 27 species per cell) and as low as -0.29 (or 0.51 species per cell). Slope z shows a similar pattern (Figure 10c), except that the relationship is inverted and there is a proportionally lower z for some of the eastern peripheral sub-regions (Kouga, Tsitsikamma). The inverted relationship between $\log(c)$ and z is expected because they are inversely correlated (see above).

However, even residuals show a strong spatial signal (Figure 11). The residual of the slope z as predicted by the intercept $\log(c)$ (Figure 11a), shows a very strong southwestern over-prediction, with a radial decrease outwards towards a strong under-prediction in the north and especially the east. The residual of richness as predicted from the intercept $\log(c)$ (Figure 11b) shows

an over-prediction on the species-poor periphery of the CFR, with an under-prediction in the southwest. By contrast, the residual of richness as predicted from the slope z (Figure 11c), shows an under-prediction in the species-poor eastern portion of the CFR and an over-prediction on the species-poor western and northern regions.

Apart from the broad patterns, a fine-scale signal also exists. An inspection of the contiguous areas (blocks) of Fynbos shows that the residual of slope z as predicted by intercept $\log(c)$ (Figure 11a), is greater on the edges in the south-west and northwards, but lower on the edges in the east. The residual of species richness predicted $\log(N)$ from the intercept $\log(c)$ (Figure 11b) also shows that the edges of the blocks are under-predicted in the south-west, and over-predicted in the east, although the pattern is not as distinct as previously. However, the residual of species richness as predicted by slope z (Figure 11c), shows a consistent pattern of over-prediction on the edges of blocks, and under-prediction at their centres.

A perusal of the spatial signal for these same parameters for data sets truncated at the edges of subregions (Figure 12) reveals that these patterns are not a feature of the CFR, but are determined by the termination of the data sets (i.e. whether at sub-region or CFR boundary). In each case, exactly the same patterns of over-prediction and under-prediction, both regional and fine-scale and for each parameter, found for the entire CFR are now found within each sub-region.

Discussion

Almost every point we wish to make in discussing these results can be illustrated by reference to Figure 2. What is seen very clearly is that the (A, S) data pairs fill a clearly delineated region, more or less triangular, on the log-log plot. Two points stand out:

1. the tendency of species number to increase with area is apparent from upper and lower boundaries of the scatterplot, which both have positive slope, and
2. the variance in S is large for small A and small for large A.

Figure 3 illustrates similar data for counts internal to the sub-regions; they exhibit the same two features noted above. The 29 (A, S) pairs for the area and number of species of each sub-region plotted in Figure 4 again repeats this pattern.

A species-area curve for Proteaceae in fynbos would summarise all these scatterplots in a single formula; if we use $S = cA^z$ then Figure 2 leads us

to $z = 0.47$ via a least-squares fit. This value has independent support from the sub-regional counts in Figure 4, where $z = 0.50$ is obtained. We note that the nested tetrad z values in Figure 5, while also consistent with Figure 2, do not amount to an independent confirmation, as Figure 2 is the superposition of these nested data sets, which are pair-wise disjoint and each contain one (A, S) pair from each focus level.

So is the CFR characterised by $z \approx 0.5$? Unfortunately, our data give conflicting values. First, if we use all tetrads internal to the sub-regions, we get the distinctly lower estimates of Table 1. On the other hand, for (A, S) pairs taken from a single focus level, the values of z are very much higher, quite inconsistent with $z \approx 0.5$. Nevertheless, they are consistent with each other, and support a value of $z \approx 1$, on $k' \times k'$ tetrads for a fixed k. These inconsistencies appear to reflect differences in the sampling schemes: in the cases where $z \approx 0.5$, the values of A span much larger intervals than in the cases where $z \approx 1$. However, this cannot be the full explanation, since a simple vertical slice over a relatively narrow range $[A, A+\delta A]$ in Figure 2 would yield an estimate of z consistent with $z \approx 0.5$. Instead, it appears that the data for such an $[A, A + \delta A]$ slice comes from several focus levels, and that the higher values of S come from focus levels with smaller k. Thus within focus levels there is a strong bias against tetrads with small A and large S; we are unable to suggest an explanation for this bias.

The foregoing tends to undermine our confidence in the validity of estimates of z, and the huge variance in S at low A makes things no better. It causes variability in the nested tetrad estimates, as follows. Every nested tetrad data set in Figure 2 starts with a $1' \times 1'$ cell with an (A, S) pair that lies on the $\log(c)$ axis, and then moves along a non-decreasing line to a $1023' \times 1023'$ tetrad containing the whole fynbos. They all end at the same (A, S) pair, and therefore lines that start with high S must climb more slowly than lines that start at low S. Thus the high variance of S at low A not only means that $S = cA^z$ is subject to large error at low A, but also that nested sampling schemes will yield negatively correlated estimates of $\log(c)$ and z, as is reported in Figures 7 and 9. Moreover, the wider the range of richness at low A, the wider will be the range of estimates of $\log(c)$ and z.

The correlation of $\log(c)$ and z with $\log(S)$ accounts for the similarity in their spatial variation displayed in Figure 10. But since the residual is not random, as shown in Figures 11 and 12, there is an additional, purely spatial effect. It appears to make a difference whether the focal cell of nested tetrads is near or far from an extremity of fynbos. This is true at the relatively small scale of transitions between fynbos and other vegetation types within the CFR

as well as the larger scale of the CFR as a whole. We noted above that at a given A, the larger values of S tend to come from tetrads with smaller k. Now, for two tetrads of different k to have similar A it is necessary for the fynbos cells to fill the larger tetrad less densely; this is often the case near the boundaries of the fynbos biome at small and large scale. It seems that the relation between $\log(c)$ and z near the edges of the fynbos biome differs from how these parameters interact away from edges.

We conclude that parameter estimates of the Arrhenius curve for Proteaceae in fynbos strongly varies in space and is subject to large sampling error. Let us briefly reflect on what this uncertainty may imply.

The classical use of $S = cA^z$ in theoretical ecology is in the comparison of otherwise very different spatial domains (Rosenzweig 1995; Lomolino 2001). We note first of all that the full, set-valued species-area relationship, as shown for example in Figure 2, could in principle be used for these comparisons. It would be cumbersome but rigorous. The data requirements for such comparisons are so onerous that in many cases the available data would not suffice, as they do not get anywhere near being exhaustive. Moreover, sampling schemes often differ among data sets. Nevertheless, the full, i.e. set-valued, species-area relationship would enable comparisons of the classical kind and even support statistical inference. In the absence of representative and comparable set-valued species-area data, one must be cautious about conclusions based on Arrhenius parameters.

When $S = cA^z$ is to be used in conservation (as in for instance Driver et al. (2003)), there is an additional cause for caution. Reserves, by definition, have relatively small A. In species-area terms, this means that the included S may well be of high variance. It is highly unlikely that the Arrhenius formula is a good predictor of A at the scale of a typical reserve, and it will be even less so at the even smaller scale of extensions to existing reserves.

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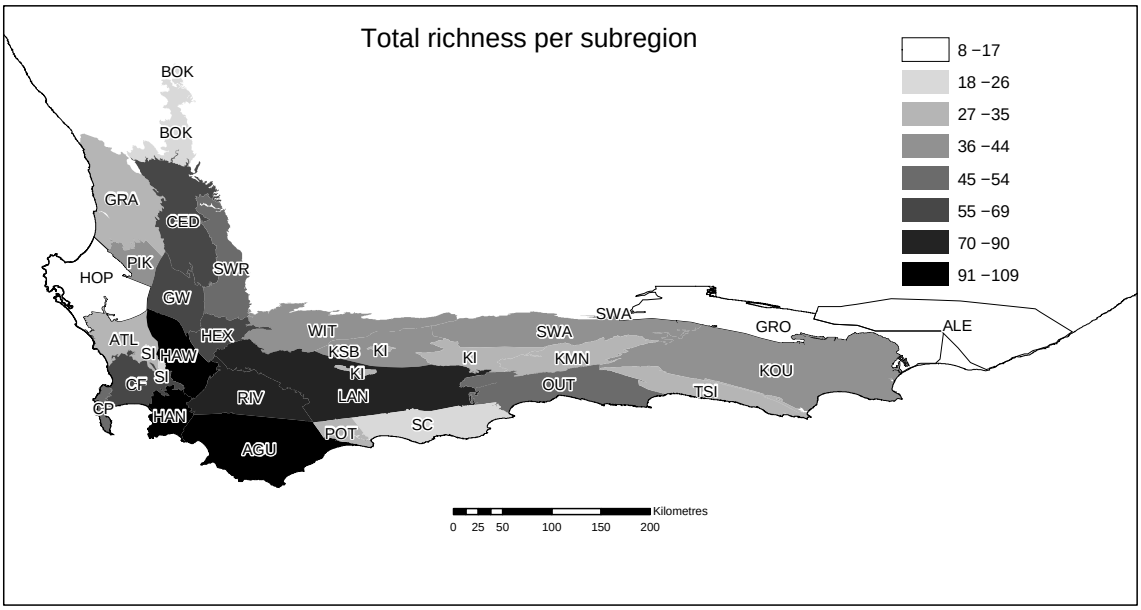
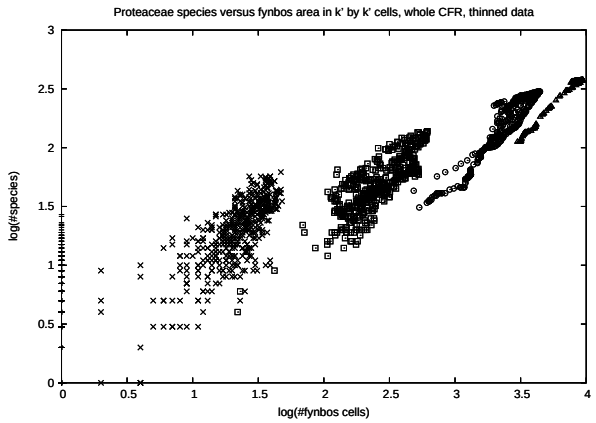


Figure 1: Sub-regions of the Cape Floristic Region, South Africa, based on centres of endemism for Proteaceae (based on Cowling et al., 1992). Fynbos areas are not shown. Boundaries are arbitrarily drawn in non-Fynbos vegetation between sub-regions. The sub-regions are classified according to the total number of Proteaceae species they contain. The sub-regions are AGU = Agulhas Plain, ALE = Alexandria, ATL = Atlantis, BOK = Bokkeveld, CED = Cedarberg, CF = Cape Flats, CP = Cape Peninsula, GRA = Graafwater, GRO = Grootrivier, GW = Groot Winterhoek, HAN = Hangklip, HAW = Hawequas, HEX = Hex River, HOP = Hopefield, KI = Karoo Islands, KMN = Kammanassie, KOU = Kouga, KSB = Klein Swartberge, LAN = Langeberg, OUT = Outeniqua, PIK = Piketberg, POT = Potberg, RIV = Riviersonderend, SC = Southern Cape, SI = Swartland Islands, SWA = Swartberge, SWR = Swartruggens, TSI = Tsitsikamma and WIT = Witteberge.

(a)



(b)

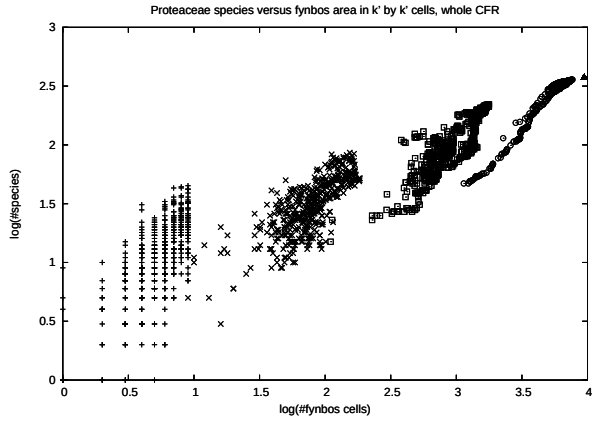


Figure 2: All the counts of k by k cells, where k = $2^l - 1$ (a) focus levels with odd l (k = 1, 7, 31, 127, 511) (b) focus levels with even l (k=3, 15,). For ease of interpretation, only every 20th datum is plotted.

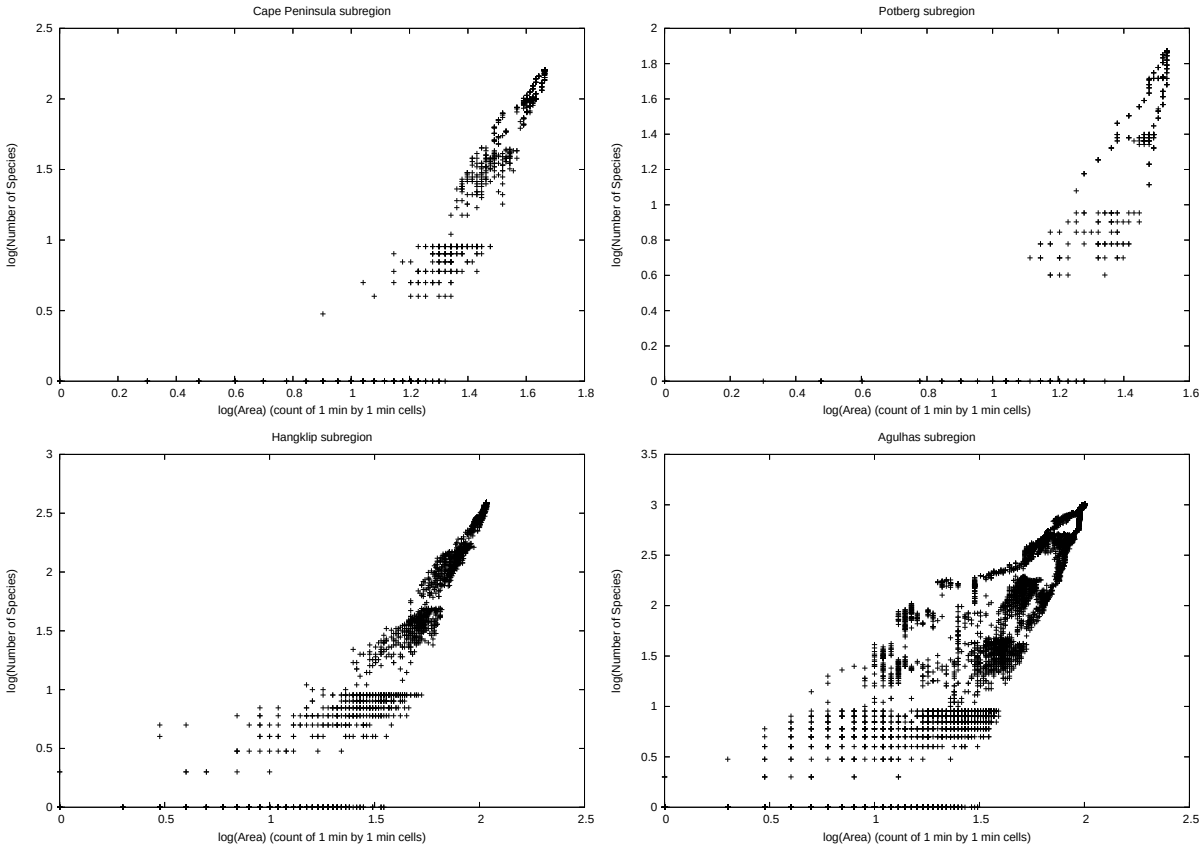


Figure 3: Representative plots, subregions: species count versus area in all $k \times k$ cells centred in the subregions Cape Peninsula, Potberg, Hangklip and Agulhas. Slope of least-squares fits are reported separately, see Table 1.

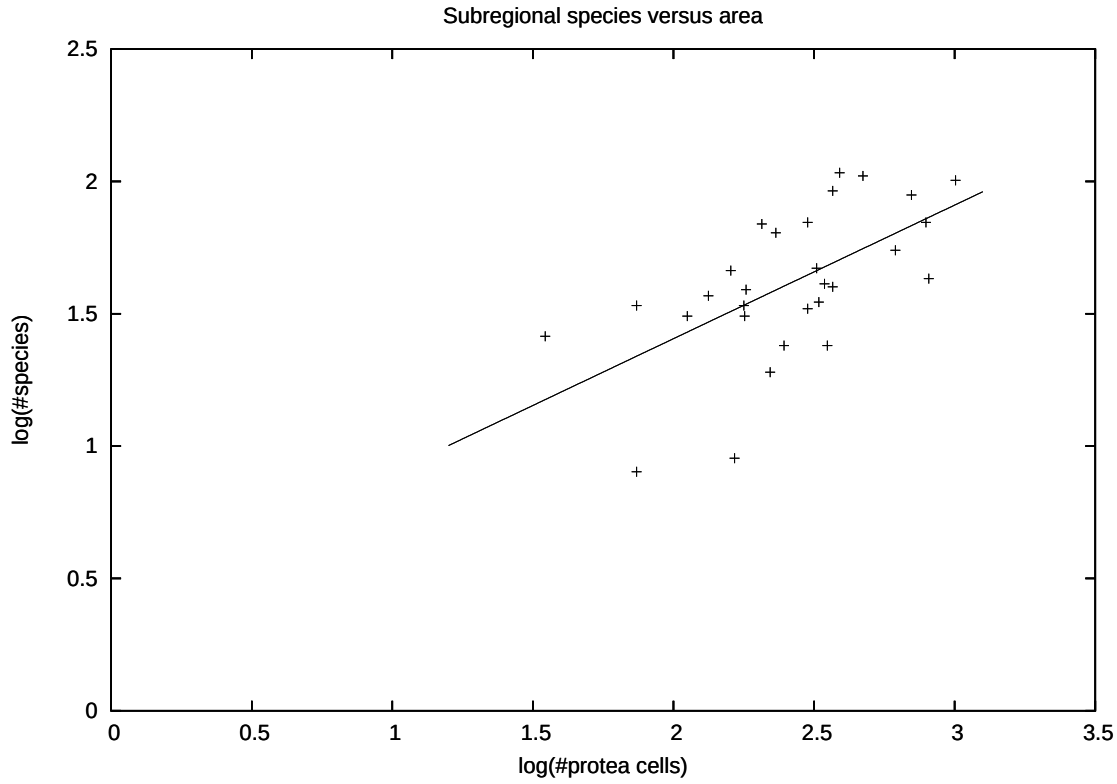


Figure 4: Species-area curve for the 29 sub-regions within the Cape Floristic Region, South Africa (the data are in Table 1). For codes and locations of sub-regions, see Figure 1. Area is the number of Fynbos cells within the sub-region (note that boundaries of sub-regions tend to lie in non-Fynbos vegetation).

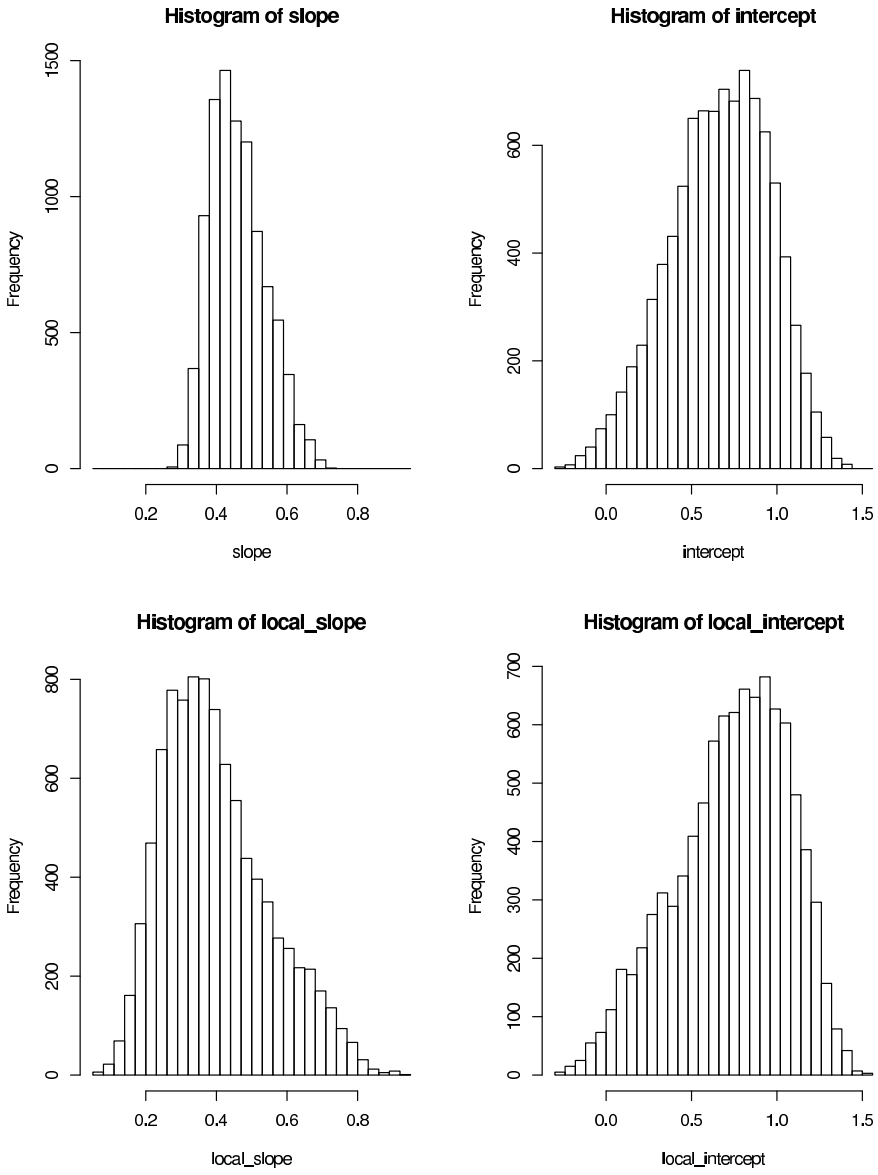


Figure 5: The distribution of slope (z) and intercept ($\log(c)$) of straight line log-log least squares fits of $N = cA^z$ to nested species-area data for Proteaceae, with focal $1' \times 1'$ cells:
(a) each series extends to entire CFR,
(b) each series is confined to one of the 29 sub-regions (Figure 1) of the CFR.
For each focal cell the species-area curve was obtained by increasing the unit area from 1 cell to 9, then to 49, 225, 961, 16129, 65025, 261121 and finally 1046529 cells, unitl the entire sub-region or CFR was sampled. Actual counts of area are below these as only Fynbos cells were counted.

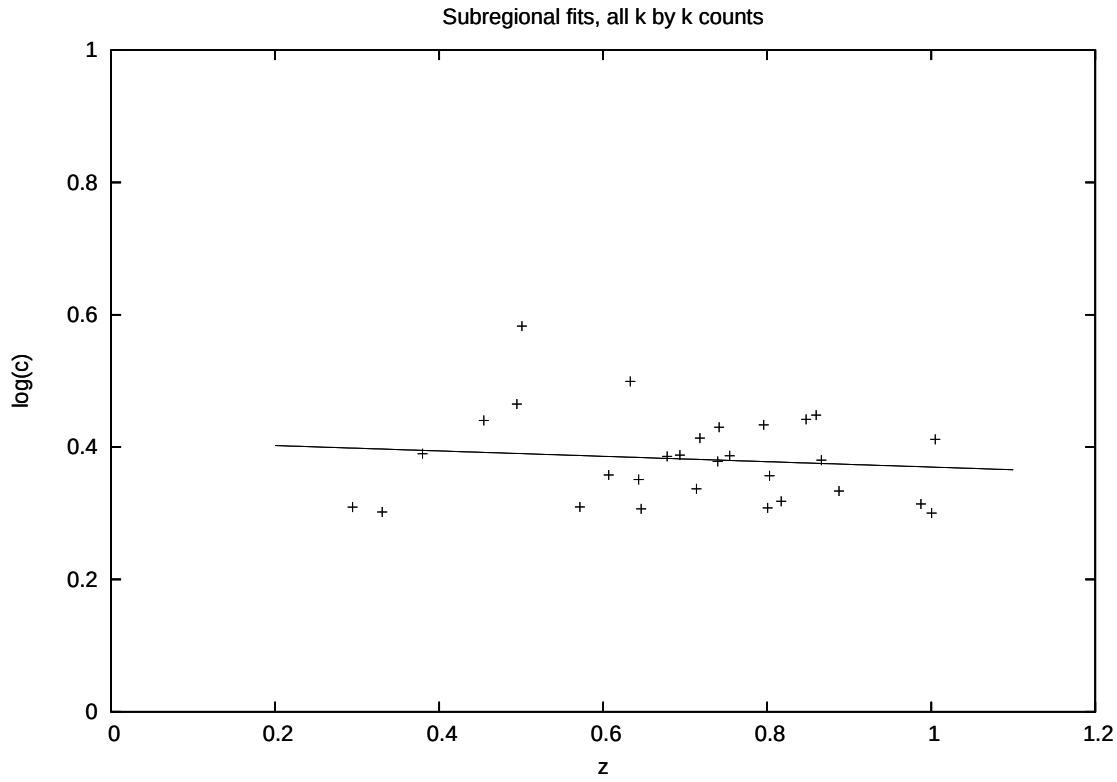
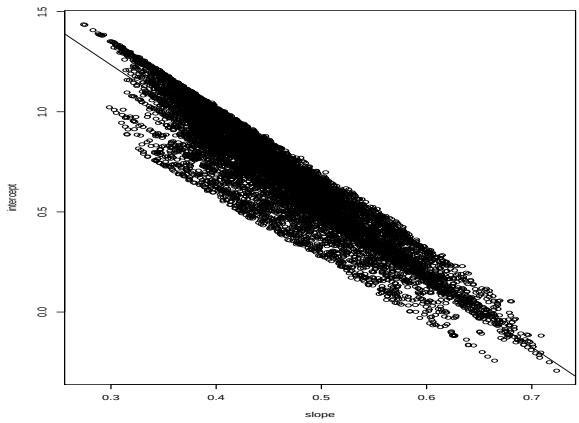
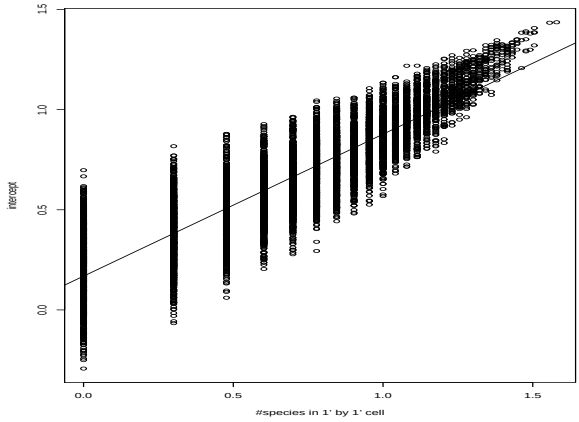


Figure 6: Correlation and variability of sub-regional $\log(c)$ and z, as estimated from all cell and unit counts in each sub-region. These values correspond to the fitted lines in Figure 3.

(a)



(b)



(c)

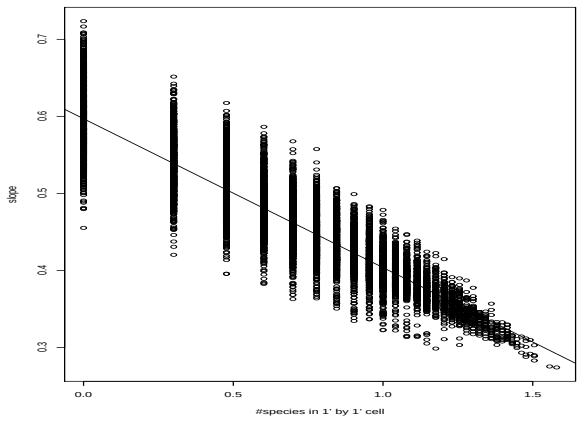
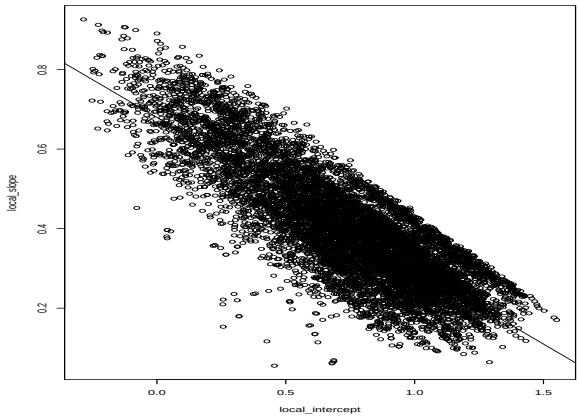
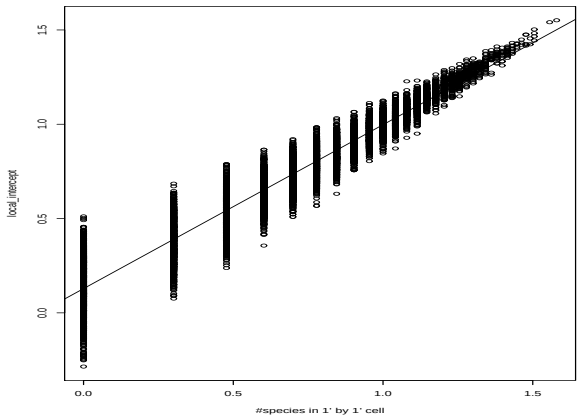


Figure 7: Slope, intercept and observed Proteaceae richness relationships for nested species-area curves of all Fynbos focal cells. All data series extend to the entire CFR. The pair-wise correlations are: (a) z vs $\log(c)$; (b) $\log(N)$ vs $\log(c)$; (c) $\log(N)$ vs z.

(a)



(b)



(c)

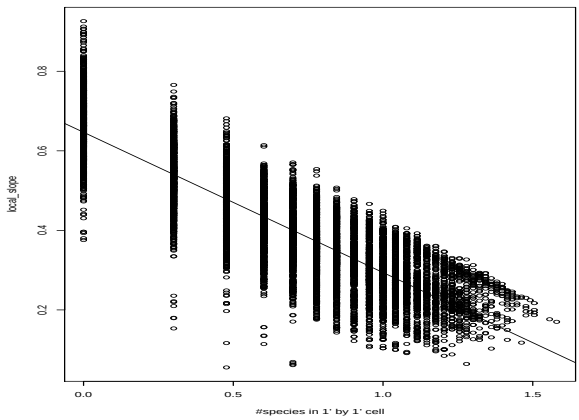
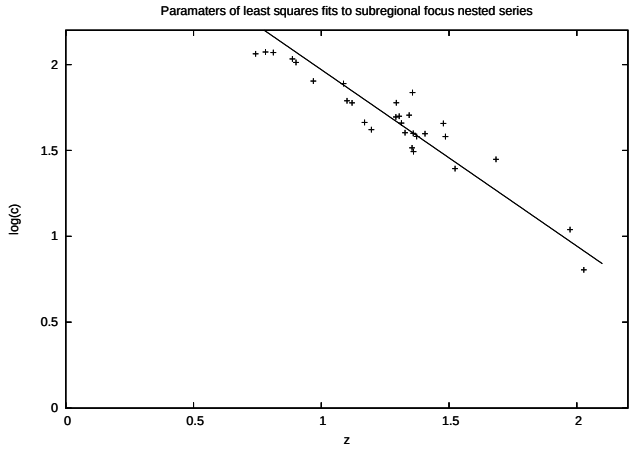
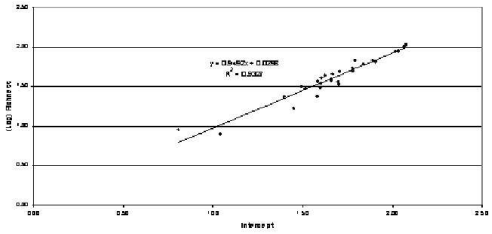


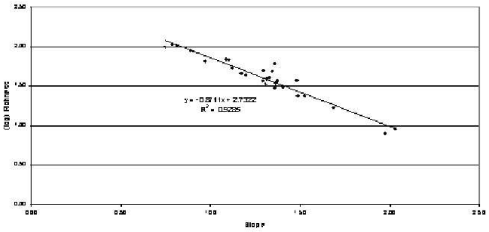
Figure 8: Slope, intercept and observed Proteaceae richness relationships for nested species-area curves of all Fynbos focal cells within the Cape Floristic Region. Each data series is confined to a single sub-region (Figure 1). The pair-wise correlations are: (a) z vs $\log(c)$; (b) $\log(N)$ vs $\log(c)$; (c) $\log(N)$ vs z.

(a)





(b)



(c)

Figure 9: Slope, intercept and observed Proteaceae richness relationships for species-area curves of 29 focal sub-regions within the Cape Floristic Region. Estimates from nested series constructed for each sub-region by accumulation of adjacent sub-regions. The pair-wise correlations are: (a) z vs $\log(c)$; (b) $\log(N)$ vs $\log(c)$; (c) $\log(N)$ vs z.

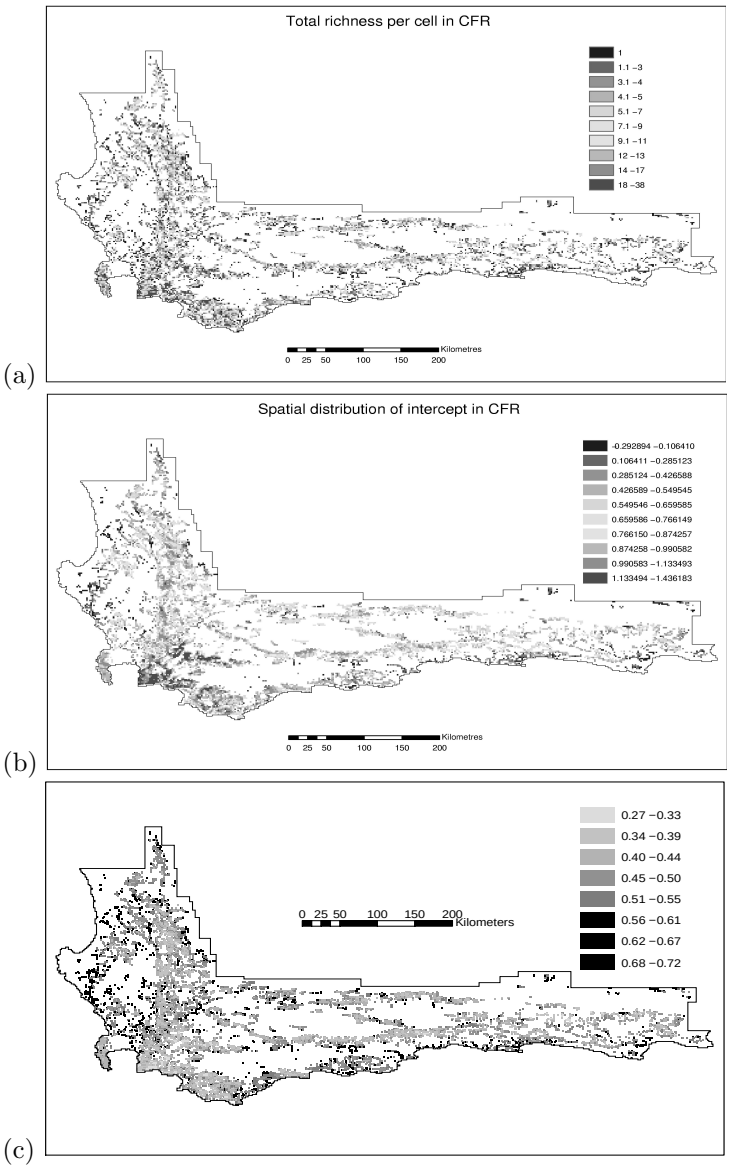


Figure 10: Spatial distribution of (a) observed Proteaceae species richness, and computed (b) intercept $\log(c)$ and (c) slope z for Proteaceae species-area curves compiled from and shown for spatially referenced data sets of the Cape Floristic Region, South Africa. Each set comprises all tetrads centred on the focal cell. Non-Fynbos cells are blank. The northern boundary is that of the Cape Floristic Region as defined by CAPE (ref? [TONY]).

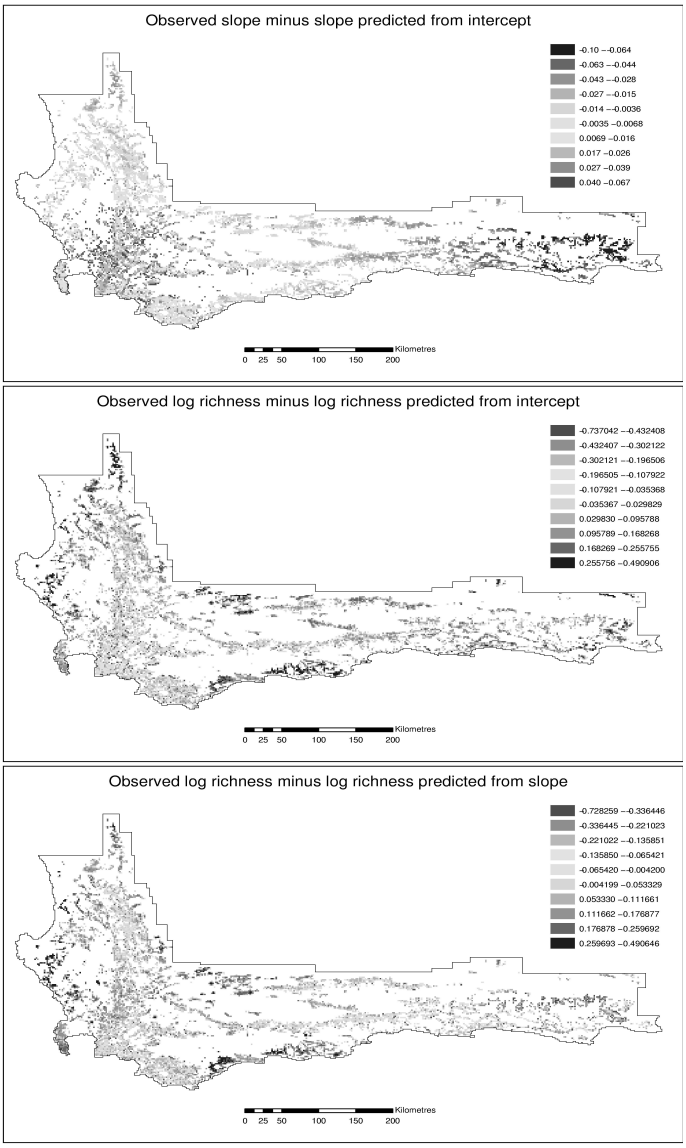


Figure 11: Spatial signal in parameter estimates of richness, slope and intercept for Proteaceae species-area curves compiled from and shown for focal cells in the entire Cape Floristic Region, South Africa. The spatial signal is determined by yobs-ypred, where ypred = k1x+k2 as a least squares fitted line, and x and y denote are defined as: (a) slope observed - slope predicted from the intercept: x = intercept c, y = slope z; (b) observed log richness - predicted log richness from the intercept: x = c, y = log (observed richness); (c) observed log richness - predicted log richness from the slope: x = z, y = log (observed richness). Non-Fynbos cells are blank.

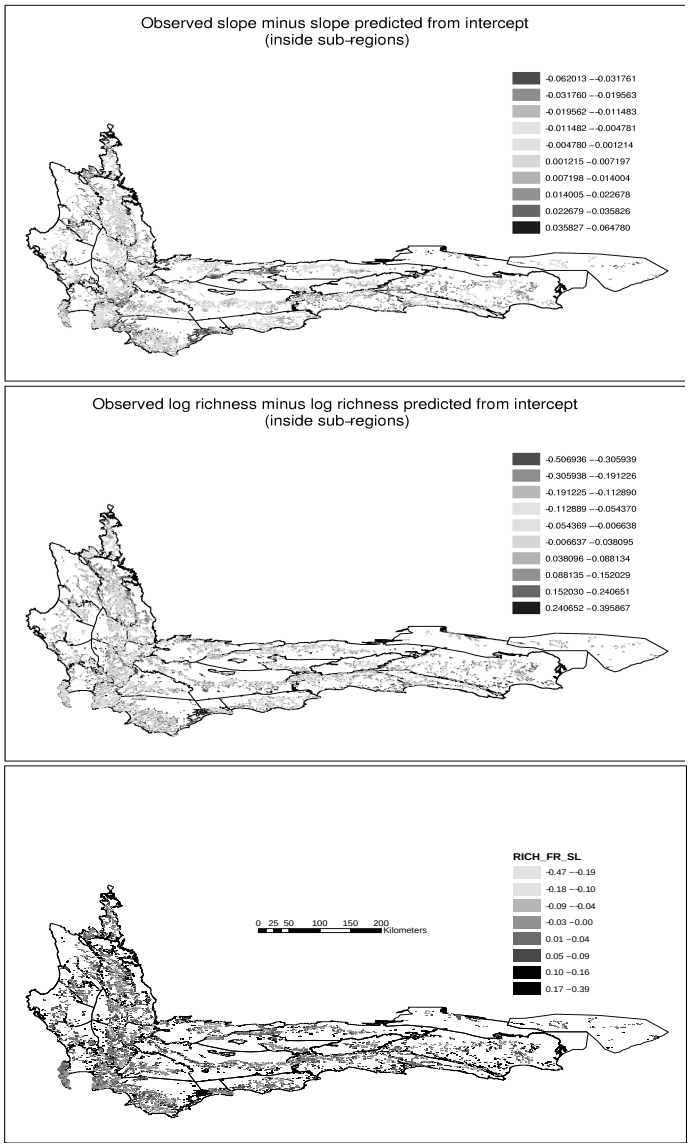


Figure 12: Spatial signal in parameter estimates of richness, slope and intercept for Proteaceae species-area curves compiled from and shown for focal cells in the sub-regions of the Cape Floristic Region, South Africa. The spatial signal is determined by yobs-ypred, where ypred = k1x+k2 as a least squares fitted line, and x and y are defined as: (a) slope observed - slope predicted from the intercept: x = intercept c, y = slope z; (b) observed log richness - predicted log richness from the intercept: x = c, y = log (observed richness); (c) observed log richness - predicted log richness from the slope: x = z, y = log (observed richness). Non-Fynbos cells are blank. Sub-regions are shown. Colour ramping is from red (underestimated) to blue (overestimated) in all cases.

List of Tables

Subregion	Area (= count of $1' \times 1'$ cells)	z	$log(c)$
Agulhas	8048	0.38022	0.86608
Alexandria	1485	0.30936	0.29435
Atlantis	1246	0.46501	0.49470
Bokkeveld	1729	0.30660	0.64631
Cedarberg	6328	0.38688	0.75419
Cape Flats	1442	0.58291	0.50089
Cape Peninsula	960	0.31396	0.98742
Graafwater	2303	0.44031	0.45436
Grootrivier	592	0.30194	0.33062
Groot Winterhoek	2100	0.43367	0.79579
Hangklip	2340	0.41171	1.00479
Hawequas	3304	0.44184	0.84747
Hexrivier	1617	0.49918	0.63303
Hopefield	1547	0.38990	0.37964
Karoo Islands	1432	0.30803	0.80056
Kammanassie	784	0.37823	0.73961
Kouga	7290	0.35791	0.60674
Klein Swartberge	1267	0.35665	0.80276
Langeberge	6318	0.43006	0.74135
Outeniqua	4920	0.38602	0.67807
Piketberg	798	0.41346	0.71795
Potberg	444	0.30028	1.00039
Riviersonderend	2576	0.44838	0.85969
South Cape	2816	0.30941	0.57158
Swartland Islands	175	0.33352	0.88746
Swartberge	2752	0.31803	0.81702
Swartruggens	2584	0.38791	0.69350
Tsitsikamma	2400	0.35086	0.64313
Witteberge	2944	0.33690	0.71363

Table 1: Subregions, overall picture: values of $\log(c)$ and z for each subregion, obtained for each subregion by linear least squares fit to log(count) of area and species for $k \times k$ cells with focal cell in that subregion. (see Figure 3 for illustrative plots).