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On the Identification of Areas of Endemism

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What are the smallest areas of the world that house endemic species—how many are there, and where are they? We have only fragments of an answer, but it looks as though there are many local areas of endemism, each defined by the overlap of two or more species ranges.

-Platnick (1992:20)

Methodological developments in cladistic biogeography have mostly focused on converting taxon-area cladograms into area cladograms and on obtaining general area cladograms (Nelson and Platnick, 1981; Wiley, 1988; Page, 1990; Nelson and Ladiges, 1991). The problem of identifying areas of endemism, although fundamental for any cladistic biogeographic study, has been somewhat neglected.

An area of endemism is an area of nonrandom distributional congruence among different taxa. It is identified by the congruent distributional boundaries of two or more species, where congruent does not demand complete agreement on those limits at all possible scales of mapping, but relatively extensive sympatry is a prerequisite (Platnick, 1991). Axelius (1991) discussed the difference between areas of endemism and areas of distribution. In studies dealing with areas situated in separate continents or islands (e.g., Crisci et al., 1991b), this distinction is apparently meaningless, but in studies dealing with taxa distributed over a continuous land mass, the correct identification of areas of endemism is basic. Although some authors (Crisci et al., 1991a; Henderson, 1991; Platnick, 1991) have recently emphasized the importance of identification of areas of endemism, there have been no proposals for identifying them in an objective way.

Müller (1973) suggested a protocol for determining areas of endemism by mapping species ranges where (1) species ranges are relatively small compared with the whole region itself, (2) their distributional limits are accurately known, and (3) the validity of the species is not in dispute. According to this approach, substantial overlap in ranges of two or more species determines an area of endemism. When dealing with a few species, Müller's approach may be easily applied by hand, but with a large number of species, difficulties arise. A way to choose which species to map so as to maximize the number of species contributing to each area of endemism would be useful.

The purpose of this paper is to explore the possibility of applying a parsimony method to delimit areas of endemism. This method is based on the parsimony analysis of endemicity (PAE) developed by Rosen (1988). PAE basically unites areas based on their shared species and proposes common historical causes to explain these groupings. PAE can be modified to help identify areas of endemism by using quadrats as operational units and employing the sets of quadrats as a base for choosing the species to be mapped. This approach, herein applied to the distributions of species of the South African weevil genus Sciobius Schoenherr (data taken from Schoeman, 1983), comprises the following five steps.

- 1. Draw quadrats on a map of the region to be analyzed, considering quadrats only where at least one locality of one species exists.
- 2. Construct a data matrix, where columns represent the species and rows represent the quadrats. An entry is 1 if a species is present and 0 if it is absent. A

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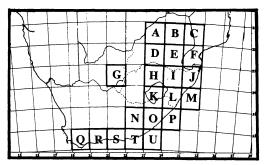


FIGURE 1. Map of South Africa, showing the 21 quadrats (A-U) used in the analysis.

hypothetical quadrat coded 0 for all columns is added to root the tree.

- Perform a parsimony analysis of the data matrix.
- 4. Delimit the groups of quadrats defined by at least two species.
- Superimpose the groups delimited in the cladogram onto the quadrats and map the species endemic to each group of quadrats to delineate the boundaries of each area.

Twenty-one quadrats were drawn in the area analyzed (Fig. 1), and a data matrix with 47 Sciobius species was constructed (Table 1). The analysis with options mhennig* and bb* of Hennig86 (Farris, 1988) produced 289 cladograms (72 steps, consistency index = 0.65, retention index = 0.67). In the strict consensus (Fig. 2), two groups are defined by, respectively, two and five species: (1) J + M + I + L and (2) S + R + N + O + T. Quadrat P, which has seven endemic species (=autapomorphies), is equivalent to a group of quadrats (group 3 in Fig. 2). By mapping species endemic to the groups, the three areas of endemism of Figure 3 result.

Although the extension of the quadrats to be considered in step 1 is difficult to assess a priori, an additional step could be added when the five steps have been completed. In this step, the original quadrats involved in conflicting relationships with more than one of the delimited areas could be further subdivided into smaller units and then the procedure repeated.

When dealing with distributions of

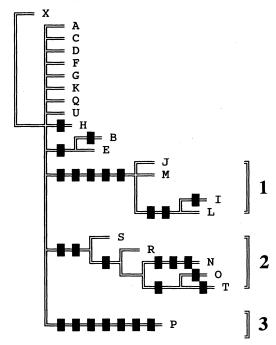


FIGURE 2. Cladogram of the quadrats obtained from the analysis of the data matrix of Table 1. Bars indicate apomorphic changes.

widespread species, they could overlap and generate many equally parsimonious cladograms. The strict consensus tree, however, preserves the most robust groupings of quadrats, thus minimizing the influence of widespread species.

The rationale for lumping quadrats is illustrated by the first group. Although I + L are united by two species, neither J nor M have at least two species endemic to

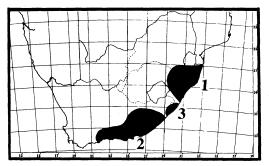


FIGURE 3. Areas of endemism based on the groups from the cladogram in Figure 2.

TABLE 1. Data matrix of *Sciobius* species \times quadrats (areas) (A–U, see Fig. 1; X = root). Columns and rows have been transposed for presentation.

| Species | Quadrats | | | | | | | | | | | | | | | | | | | | | |
|----------------|----------|---|--------|---|---|---|---|---|---|---|--------|---|---|---|---|---|---|---|---|---|---|---|
| | X | Α | В | С | D | Е | F | G | Н | I | J | K | L | M | N | 0 | P | Q | R | S | T | U |
| aciculatifrons | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| angustus | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| anriae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| arrowi | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| asper | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| barkeri | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| bistrigicollis | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| brevicollis | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| capeneri | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| cinereus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| cognatus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| cultratus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| dealbatus | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| endroedyi | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| granipennis | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| granosus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | ō | Õ | Ō | ō | ō |
| griseus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | ō | ō | 1 | ō | 1 | ō |
| holmi | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | ō | ō | ō | ō | ō | Ō | ō | ō |
| horni | ō | 0 | 0 | 0 | 1 | Õ | ō | 1 | 1 | ī | ī | 1 | 1 | Õ | Õ | Õ | ŏ | Õ | Õ | ŏ | ŏ | ŏ |
| impressicollis | 0 | 0 | 0 | 0 | 0 | 0 | ō | ō | ō | ō | ı 1 | ō | 1 | Õ | Õ | Õ | 1 | Õ | Õ | Õ | Õ | Õ |
| kirsteni | Ö | Õ | Õ | Õ | Ö | ŏ | Õ | Ö | 1 | ő | ô | Ö | ô | ő | ő | ő | ô | ő | ő | ŏ | ő | ő |
| lateralis | Ö | Õ | Õ | Õ | Ö | Õ | Õ | ŏ | õ | Ö | ŏ | Õ | Ö | ŏ | ŏ | ő | 1 | ő | ő | ŏ | ő | ő |
| marginatus | Ö | Õ | Õ | Õ | Ö | Õ | Õ | ŏ | ő | 1 | 1 | Õ | 1 | 1 | ő | ő | ô | ő | ő | ő | Ö | Ö |
| marshalli | Õ | 1 | 1 | Õ | Õ | Õ | Õ | ő | Õ | î | î | Õ | î | î | ő | ő | ő | Õ | ő | ő | ő | ŏ |
| minusculus | Ö | õ | õ | Õ | Õ | ő | Õ | ŏ | ő | Ô | ô | ő | ô | Ô | 1 | ő | ő | ő | ő | ő | ő | ŏ |
| nanus | 0 | ő | ő | ő | ő | ő | ő | ő | ő | ő | Ö | ő | ő | ő | 1 | ő | ő | ő | ő | ő | ő | ő |
| obesus | Ö | ŏ | 1 | Õ | Õ | ő | ő | ő | ő | 1 | 1 | ő | ő | ő | ô | ő | ő | ő | ő | ő | ő | ő |
| oneili | ő | õ | ô | ő | Õ | ő | ő | ő | ő | Ô | Ô | ő | ő | Õ | 1 | 1 | ő | 0 | 1 | 1 | 1 | ő |
| panzanus | ő | ő | ő | ő | ő | ő | ő | ő | Õ | 1 | ő | ő | 1 | Õ | Ô | Ô | ő | 0 | Ô | Ô | Ô | ő |
| peringueyi | 0 | ŏ | 1 | ő | ŏ | 1 | ŏ | ő | ő | Ô | Ö | ő | Ô | ő | ő | ő | ő | ő | ő | ő | ő | ő |
| planipennis | 0 | ő | Ô | ő | ŏ | Ô | ŏ | ő | ő | ő | Ö | ő | ő | ő | ő | ő | 1 | ő | ő | ő | ő | ő |
| pollinosus | 0 | ő | Ö | ő | ő | 0 | 0 | 0 | ő | ő | 0 | 1 | 1 | 1 | 0 | 0 | Ô | 0 | 0 | 0 | 0 | 0 |
| pondo | 0 | ő | Ö | ő | ő | 0 | 0 | 0 | ő | ő | 0 | Ô | 0 | Ô | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| prasinus | 0 | Ö | Ö | ő | ő | 0 | 0 | 0 | ő | 1 | 0 | 0 | 1 | 1 | 0 | 0 | Ô | 0 | 0 | 0 | 0 | 0 |
| pullus | 0 | Ö | Ö | ő | Ö | 0 | 0 | ő | ő | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 |
| scapularis | 0 | ő | ő | ő | ő | 0 | 0 | 0 | ő | Ô | Ô | Ô | 0 | 0 | 0 | 1 | Ô | Ô | 0 | 0 | 1 | 0 |
| schoenlandi | 0 | Ö | Ö | ő | Ö | 0 | 0 | 0 | ő | ő | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | Ô | 0 |
| scholtzi | 0 | ő | Ö | ő | ő | 0 | 0 | 0 | ő | ő | 0 | ő | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| spatulatus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| tenuicornis | 0 | 0 | 0 | Ö | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| thompsoni | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| tottus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 |
| transkeiensis | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| viduus | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| viridis | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 0 | 0 | - | - | - | 0 | - | 0 | 0 | 0 | 0 | - | - | - | - | - | - | - | - | - | | - |
| vittatus | 0 | 0 | 1 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| wahlbergi | U | U | U | U | U | U | U | U | U | 1 | 1 | U | 1 | 1 | U | U | U | 0 | U | U | 0 | 0 |

each, so the four quadrats must be kept together.

Once the areas of endemism are defined, we can ask about their generality. To test their significance, several procedures could be applied, e.g., bootstrapping (Felsen-

stein, 1985), tests of permutation tail probabilities (Archie, 1989; Faith and Cranston, 1991), and skewness of the distribution of tree lengths (Huelsenbeck, 1991). These procedures, however, have been severely criticized by Carpenter (1992). An alter-

native approach would be a congruence analysis comparing these areas with those defined by similar analyses of other taxa.

The delimitation of areas of endemism is of significance in cladistic biogeography. What else could be more important than the units in any study? Parsimony methods for identifying these areas are a promising potential field for future developments. I hope this proposal will encourage others to investigate this matter.

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