Ann. Zool. Fennici 24:165–178. 1987

Recent methodological developments in quantitative descriptive biogeography

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Birks, H. J. B. 1987: Recent methodological developments in quantitative descriptive biogeography. — Ann. Zool. Fennici 24:165–178.

The use of quantitative methods in the exploratory analysis of complex biogeographical data is discussed in terms of delimiting biotic elements and biotic regions. The various stages in a quantitative analysis of biotic elements are described and recent methodological and mathematical developments are outlined, in particular problems of defining scales, appropriate proximity measures, choice of partitioning techniques, display of results, distortion tests, and evaluation of results. Future developments are suggested for comparing biogeographical regionalisations, for using spatially contrained partitionings, for developing statistical approaches in analytical studies, and for improving data-extraction techniques. The importance of critical selection and use of numerical procedures is emphasised. Current quantitative procedures, if used carefully, have the potential to link descriptive and analytical approaches to biogeography.

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1. Introduction

In the last 20 years there has been an increasing use of quantitative, computer-based methods in biogeography, particularly for descriptive and, to a lesser extent, analytical (*sensu* Ball 1975) purposes. Biogeography, particularly in its initial descriptive phase, is concerned with devising adequate and useful classifications of biogeographical patterns based on known distributions of taxa within the geographical area of interest. Just as in numerical taxonomy and descriptive ecology, quantitative techniques can assist in deriving such classifications in a repeatable and potentially unbiased way.

Computer techniques can be useful in several different ways within biogeography, for example for data-extraction, data-storage, map-production, data-analysis, simulations, and hypothesis-testing. Here I concentrate on quantitative *analysis* of complex biogeographical data consisting of presence/absence (+/–) or, more rarely, quantitative data for many, say *m*, taxa in several, say *n*, areas. The major purpose of such analysis is to detect any general, repeatable patters, so-called "structure", within the data, in the form of biotic elements (groups of taxa with similar distributions) and biotic regions (groups of areas with similar biotas). This exploratory data-analysis results in a simplification and description of the original $m \times n$ data in terms of a smaller number of elements and/or regions. This simplification can be used to generate hypotheses about causes and origins of these patterns that may subsequently be tested experimentally, compared with independent data (e.g. geological history), or incorporated into predictive models. Quantitative descriptive biogeography thus leads logically from an exploratory, hypothesis-generating phase to an analytical, confirmatory, hypothesis-testing phase (Birks 1976), and can help not only in detecting but also in explaining patterns central to Buffon's Law in biogeography, namely that different areas support different biotas.

Delimitation of biotic elements and regions is valuable for several reasons. (1) It is useful to group taxa of similar distributions because physiological studies on, for example, climatic tolerances need not be considered in isolation but related to other taxa with similar or contrasting distribution. (2) It is important to see which patterns are common to several groups (e.g. birds, plants, butterflies) and hence likely to be of regional significance and which are unique to particular groups by comparing geographical patterns or "regionalisation" of biotic regions for different groups (e.g. Järvinen & Väisänen 1980). (3) It can be valuable to see where biotic elements overlap in distribution and hence which areas contain a range of elements and would merit conservation on the grounds of *biogeographical* diversity.

The aims of this paper are (1) to outline briefly the main aims of quantitative biogeography and the reasons for using numerical classificatory or partitioning methods in descriptive biogeography, (2) to review recent numerical developments in classification techniques that are of potential importance in quantitative biogeography, and (3) to suggest possible future developments, particularly in linking descriptive and analytical biogeography. No attempt is made to discuss specific biogeographical analyses or data-sets or to present examples of quantitative studies. The emphasis throughout is on recent developments in methodology, many of which have occurred outside biogeography and ecology, but which I think could be potentially valuable in future quantitative biogeographical analyses.

2. Main aims and interests in quantitative biogeography

Given a matrix of distributional data for m taxa in n regions with entries of 1 or 0 when species i is present or absent respectively, in region k, two major types of quantitative analysis can be recognised (Simberloff & Connor 1979, Connor 1987a). There is analysis of affinities between distributional patterns of taxa, so-called R-mode analysis, resulting, for descriptive purposes, in biotic elements, here defined as groups of taxa that have similar geographical distributions today within the geographical area of interest. The term element is used here as a purely descriptive concept, in contrast to its use by many biogeographers to refer to groups of taxa that share not only common distributions but also a (presumed) common origin and migratory, even evolutionary, history. Individualistic behaviour of taxa in time and space over the scales of interest in biogeography (e.g. Huntley & Birks 1983) appears to be the norm rather than the exception, and shows the importance of discarding historical connotations in the biotic-element concept (Fægri 1963).

The alternative type of analysis considers biotic affinities between geographical areas, so-called Q-mode analysis, with its emphasis on assessing similarities between areas and delimiting biotic regions (Simberloff & Connor 1979, Connor 1987a). Results of R- and Q-mode analyses can usefully be combined to provide insights into the structure of the original distributional data (e.g. Proctor 1967, Birks 1976, Williams 1982).

Although it is clear when perusing distribution maps that some distribution patterns recur and thus that some taxa have broadly similar distributions and belong in the same element, problems commonly arise in trying to delimit elements visually. These include (1) the tendency to detect groupings even when none are present, (2) the tendency to select certain distributions as "types" and to group other maps around them, and (3) the tendency to bias subconsciously the groupings because of preconceptions about possible causative factors (Jardine 1972, Birks 1976). Moreover, it is extremely difficult, if not impossible, to detect biotic regions visually because the primary source of biogeographical data is arranged by taxon, namely distribution maps, whereas biotic regions require distributional data arranged by area. Some form of "mental overlaying" of taxon maps is thus required to detect areas with similar biotas. This is clearly impossible if there are more than a few taxa.

Using numerical techniques to derive elements or regions overcomes many of these problems. Numerically defined elements or regions are defined solely on the basis of the original data matrix without any preconceptions about causative factors, and thus avoid any subconscious bias and problems of the typological approach. Quantitative techniques, given the same data and algorithm, produce consistent, repeatable results. Moreover, they force us to be explicit about aims, assumptions, and methods and require data sets to be constructed in a uniform way based on a standard taxonomy (Birks 1976).

It is important to emphasise that numerical methods make *no* claim to be objective (Gordon 1981, Birks & Gordon 1985). Many subjective decisions have to be made prior to any numerical analysis. However, once these decisions are made, the results are repeatable. No numerical analysis should become an end in itself; it is a means to an end. The use of each analysis should be carefully evaluated and its value assessed to obtain maximum efficiency in data-handling. It is the interpretation of the results that is the important but difficult part of quantitative biogeography. No amount of computing, however skilful, can compensate for a first-hand knowledge of the biogeography and ecology of the taxa concerned.

3. Numerical analysis of distributional affinities between taxa (R-mode analysis)

Ten stages in the numerical analysis of biogeographical data in terms of delimiting biotic elements can be distinguished (Fig. 1).

3.1. Definition of initial aims and interests

As in any scientific study, it is necessary to define clearly at the outset the aims and interests of the study and its geographical and temporal scales. Such an aim might, for example, be the delimitation of biotic elements within the ant fauna of Europe based on available distribution maps for Europe.

3.2. Delimitation of geographical units and their scale within the region of interest

This stage involves two parts — (1) selection of the type of geographical units to be used for data compilation, and (2) definition of the appropriate scale of the geographical units.

Arbitrary areas within the region of interest can be used, such as countries, counties, latitude/longitude blocks of equal size, individual 50×50 km squares of UTM grid maps, etc. These units should be selected strictly on geographical criteria only, without consideration of ecological or biological factors, to avoid any circular reasoning (Jardine 1976).

Problems of defining the appropriate scale of the geographical units can arise (Jardine 1976). If the areas are very large, the resulting patterns and biotic elements will be correspondingly broad, whereas if the areas are very small, problems of uneven recording can influence, to a disproportionate extent, the final groupings and may even fail to reveal the major underlying patterns because of a high "noise" to "signal" ratio in the data.

There is no guarantee that elements delimited from a data set using small areas will be similar to those detected when larger areas are used. Phipps & Cullen (1976) obtained very different results for 32 *Papaver* species in Turkey when 50×50, 100×100, and 200×200 km grids were used. Hengeveld & Hogeweg (1979) compared carabid elements at two geographical scales, The Netherlands and Europe, using 10×10 and 500×500 km grids, respectively. They showed that patterns for Dutch carabids at these two scales are different but not independent. At the scale of The Netherlands the resulting elements are primarily habitat-related, whereas at the broader European scale they are more closely linked to macroclimate.

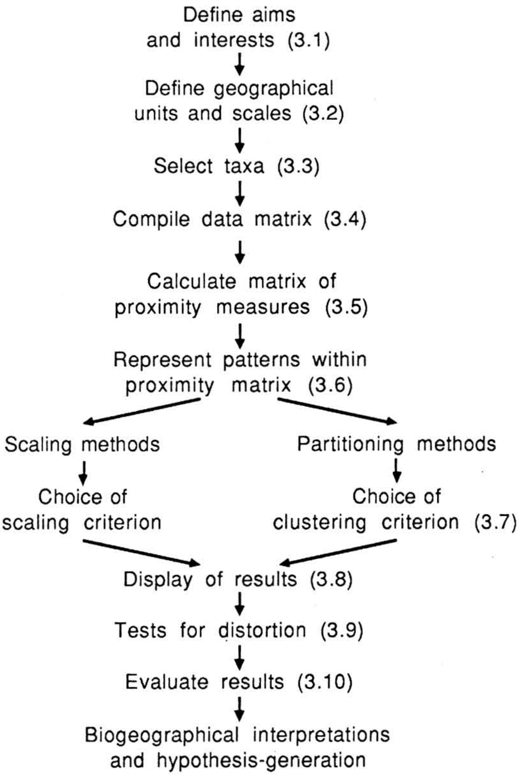

Fig. 1. Stages in the numerical analysis of biogeographical data. The numbers refer to sections in the paper where the particular stage is discussed.

Choice of scale of geographical units within the region of interest is thus a critical decision. The "bestblock" method (Phipps 1975) is useful for estimating an optimal scale, defined as the one that maximises the number of matches in +/– comparisons over all pairwise comparisons. Although bestblock is not perfect, it helps to make scale selection less arbitrary than otherwise.

3.3. Selection of taxa

The basis of any biogeographical analysis is an adequate taxonomy. It is important that the taxonomic treatment of the group in question should be as uniform as possible between taxa and between areas.

Clearly it is essential to avoid comparing taxa in one area delimited by taxonomic "splitters" with taxa in another area defined by "lumpers". When analysing biogeographical data from a large region (e.g. continental scale), such taxonomic problems are difficult to avoid unless there is a standardised taxonomic treatment for the whole region.

Further taxonomic problems can arise in analyses based on native taxa only, as all records of introductions should be correctly evaluated and eliminated (Jardine 1972). In order to avoid bias, *all* taxa in the group of interest occurring in the region should be included and given equal weight in the numerical analysis. If the data set is large, it can be usefully subdivided randomly, and the patterns detected in one subset tested against the patterns in the other subset.

3.4. Compilation of data matrix

This involves tabulating occurrences of taxa in the areas within the geographical region. For discrete localities (e.g. islands), each island is a recording unit and distribution data can be extracted from literature and collections, and tabulated (Connor 1987b). For areas within a land-mass it is more difficult to compile such data. The commonest way, after selecting the recording areas, is to draw them on to transparent film, overlay this on distribution maps, and tabulate the data (e.g. Birks 1976). This is time-consuming and often difficult, particularly if the maps are drawn to different scales or projections. The data, once extracted, cannot be converted to different grid sizes for calculating bestblock estimates or elucidating effects of different scales. Connor (1987b) describes automated digitizing of distributional maps that overcomes many of these problems.

The reliability of all subsequent analysis depends on how complete and reliable the data matrix is. A further assumption is that +/– data are adequate (cf. Thaler & Plowright 1973). In some instances, taxon abundance within individual areas is available, for example as bird-census data (Bock et al. 1978, Järvinen & Väisänen 1980), proportion of area occupied (Kaiser et al. 1972), or number of smaller grid-squares occupied within the recording area.

3.5. Calculation of matrix of proximity measures

The calculation of proximity or distance measures between all pairs of objects of interest, in this case taxa, is the first part, explicitly or implicitly, or almost all multivariate data-analytical techniques. It is most useful to consider distance or dissimilarity (complement of similarities) coefficients, d_{ij}, where d_{ij} is the dissimilarity between objects i and j, because distances can be used to represent geometrically the matrix of proximity measures between pairs of taxa. As all subsequent numerical analysis is based on such a matrix rather than on the original data matrix, it is essential that the distances accurately reflect the original data. Great care is therefore needed in selecting appropriate measures (Gordon 1981).

A large number (ca. 60) of proximity measures exists for binary +/– data (e.g. Cheetham & Hazel 1969, Lamont & Grant 1979, Gower 1985), several of which are very similar or even synonyms, whereas others do not obey the basic mathematical requirements for a symmetric proximity measure. Many coefficients include a term for joint absences of variables (e.g. simple matching and Rogers & Tanimoto indices — see Gower 1985). In biogeography, such co-absences convey little useful information and there is no reason why, when comparing distribution of taxa, the areas where neither taxon occurred should contribute to the proximity measure (cf. Baroni-Urbani & Buser 1976).

Hubalek (1982) presents a useful analysis of 43 coefficients in terms of admissible theoretical criteria and concludes that the Jaccard, Kulczynski, Dice-Sørensen, and Driver-Kroeber-Ochiai similarity measures and their dissimilarity complements "generally work well". Another useful coefficient is Baroni-Urbani & Buser's (1976) measure, but unlike the others recommended by Hubalek this incorporates, to a small degree, joint absences. Hubalek concludes that "three or so alternative coefficients should be used and the results compared; moreover significance tests should be carried out whenever possible".

In the case of the Jaccard and Baroni-Urbani & Buser coefficients, something is known of their statistical properties (see Baroni-Urbani & Buser 1976, Hendrickson 1979, Baroni-Urbani 1980) and the approximate statistical significance of observed values can be evaluated at a given probability level (see Johnson & Millie 1982, Rice & Belland 1982, Strauss 1982 for other evaluation aproaches for proximity measures). In general all these measures are descriptive in character and are acceptable for descriptive exploratory data-analysis. Probabilistic measures for R-mode (taxon × taxon) analysis are rare. Williams (1944) proposed such an index (number of taxa present in two areas / number of taxa expected from a species-area curve if the areas were random, independent samples of the same homogeneous region). This is an R-mode analogue to the probabilistic coefficient for Q-mode analysis of Connor & Simberloff (1978), Simberloff (1978), and Raup & Crick (1979).

3.6. Representation of patterns within the distance matrix

There are two general approaches for representing such patterns: (1) to display the objects, in this case taxa, as points in low-dimensional space (usually 2 or 3 dimensions) so that objects that are similar to each other in the distance matrix are represented by points close together, so-called ordination or scaling (e.g. Gower & Digby 1981, Gordon 1981, Everitt 1978, Everitt & Dunn 1983, Jambu & Lebeaux 1983), and (2) to impose a partition on the data, dividing the objects into g disjoint groups so as to optimise some stated mathematical criterion, so-called partitioning or numerical classification (e.g. Everitt 1980, Gordon 1981, Jambu & Lebeaux 1983). Although both approaches can be useful in biogeography (e.g. Proctor 1967, Holloway & Jardine 1968, Birks 1976, Baroni-Urbani & Collingwood 1977), for descriptive purposes partitioning results are most relevant.

In partitioning techniques the number of groups, g, is unknown at the outset. In theory, optimal partitions are sought for different values of g, and the results assessed. There are very many ways of partitioning n objects into g groups. However, current programming techniques are such that it is not computationally feasible to identify with *certainty* the partition that is globally optimal with respect to a particular clustering criterion. Approximating algorithms thus have to be used. These fall into two main types. (1) Agglomerative algorithms where initially there are n groups, each with one object. At each cycle, pairs of groups are amalgamated that are most similar in terms of the clustering criterion used, thereby producing a hierarchically nested set of partitions. A generalised agglomerative algorithm (Wishart 1969) exists for single-link, complete-link, group-average (weighted and unweighted), median, centroid, minimum-variance (sum-of-squares), and flexible clustering, thereby making computer implementation of all these methods easy. Such an agglomerative algorithm is, however, only an approximation to the optimal partion into g groups with respect to a particular clustering criterion. Moreover, it imposes an hierarchy on the set of partitions (e.g. the partition into 3 groups must be nested within the 2-group partition). This structure may be unwarrented for many biogeographical data sets (Van Ness 1973). (2) Iterative relocation procedures in which an initial partition into g groups is modified by relocating objects from one group to another in an attempt to improve on a clustering statistic. The procedure continues until no further improvement occurs, although even then there is no guarantee that the mathematically optimal solution has been obtained. It is computationally extremely time consuming, as it must be repeated for different initial configurations and different values of g (see Everitt 1980, Gordon 1981 for further details). With large data sets, such as occur in biogeography, the computing demands for iterative relocation procedures become so great that they are not yet computationally feasible for all but the smallest data sets.

Gordon & Henderson (1977) present a particularly useful hybrid algorithm that represents a compromise between computational demands and mathematical optimality. It invariably produces partitionings with lower total within-group sum-of-squares than its agglomerative counterpart, it does not impose a hierarchically nested classification, and it is computationally fast. It warrents wider use in biogeography.

3.7. Choice of clustering criterion

Very many partitioning procedures, all using different clustering criteria, exist (e.g. Cormack 1971, Everitt 1980, Gordon 1981, Jambu & Lebeaux 1983) and the problem facing biogeographers is to decide what procedure to use. It is important to be aware of the difficulties in selection, as they highlight the limitations of numerical classificatory procedures. Each method is well-suited to revealing particular types of data structure. For example, single-link clustering detects groups of any shape as long as they are well separated whereas minimum-variance clustering detects compact, spherical-shaped clusters (Gordon 1981). Very different partitions can result depending on the method used (e.g. Everitt 1980). If the structure of the data was known in advance, an appropriate partitioning method could then be selected to display this structure. The circularity is now clear. The structure is *not* known in advance, and partitioning methods are being used to discover what structure there is within the data. This is, after all, the function of exploratory data analysis! The problem of which clustering criterion to use is thus critical but unresolved (see Gordon 1981).

Attempts have been made to evaluate different methods by simulation studies using data-sets with known structure (e.g. Cunningham & Ogilvie 1972, Blashfield 1976, Milligan 1981). In general, there is no "best" method for all data sets. Single-link is nearly always the least successful, whereas group-average and minimum-variance generally provide useful results.

The recommended approach at present, given existing theoretical understanding of different clustering criteria, is to use several methods on the same data set. If similar results emerge, one can have more confidence that the groups have some reality and are not simply artifacts of any one method (Gordon 1981).

3.8. Display of partitioning results

There are various ways of representing numerical classification results (see Everitt 1978, 1980, Gower & Digby 1981). (1) Dendrograms or binary trees can be constructed to show the hierarchical merging of objects. This is only possible for hierarchical methods, using either an agglomerative or divisive algorithm (e.g. two-way indicator species analysis (Hill 1979) or polythetic divisions (Lefkovitch 1974)). (2) Dissimilarity-matrix shading (Ling 1973) involves re-ordering the original distance matrix into the object order suggested by the classificatory results, either from hierarchical or iterative relocation analysis, and shading the matrix in terms of the dissimilarity values. (3) Two-way matrix analysis (Birks 1976) requires partitioning both the taxa (R-mode) and areas (Q-mode) separately, re-ordering the data matrix in taxon and area order, and quantifying the concentration of elements for each taxon-area partition. It can be used with any partitioning procedure. Biogeographical examples include Proctor (1967) and Birks (1976). (4) Mapping the distribution of elements in terms of numbers of taxa occurring in each geographical area within the region of interest. Each element requires a map (e.g. Proctor 1967, Birks 1976, Baroni-Urbani & Collingwood 1976, 1977).

Methods (3) and (4) require the partitioning level and hence the number of groups (elements) to be decided before the results can be displayed. This raises the critical question of how many groups. I return to this question when considering the evaluation of the results.

3.9. Tests for distortions

This stage is rarely done, even though it is an essential step. Hierarchical partitioning procedures can be regarded as a transformation that converts the original distances between pairs of objects into new distances represented by the lowest level two objects belong to the same group in a dendrogram (Gordon 1981). Inevitably such a transformation introduces distortions. A variety of distortion measures is available (see Cormack 1971). The most widely used is Sokal & Rohlf's (1962) cophenetic correlation which is simply the product-moment correlation coefficient between the original and new distances for all $n(n-1)/2$ pairwise comparisons.

3.10. Evaluation of results

As Green (1979) warned about exploratory multivariate data analysis, "such techniques yield results that give the appearance of things going on even when applied to data simulated to be completely random... It is a wise precaution to test "nothing is going on" (as a null hypothesis) first". It is thus essential to evaluate all partitioning results critically. Current approaches are reviewed by Dubes & Jain (1979), Gordon (1981), and Milligan & Cooper (1985). Four important questions in evaluation are (1) is the data matrix random and is structure being imposed on unstructured data, (2) how well does a hierarchical nesting fit the original data, (3) which groups are valid statistically, and (4) how many groups should be recognised?

An answer to question (1) can be obtained by randomisation procedures (e.g. Harper 1978, Strauss 1982). Random (null) incidence matrices are generated within the constraints of constant row and column totals. Such constraints retain the biotic richness of areas and the frequencies of different taxa. These matrices are then subjected to cluster analysis, and the process continued many times. Any group is deemed statistically significant if its node value in a dendrogram exceeds the $(1-\alpha)$ percentile (where α may be set conventionally at 0.05) for, say 100 simulations. Strauss (1982) analysed distributions patterns of 43 fish species in a Pennsylvanian river and showed that only 7 of 12 groups were significant. This type of approach has considerable potential, as it represents an attempt to link exploratory and confirmatory data analysis and to put numerical classification on a more rigorous, statistical basis (see Birks 1985).

Cophenetic correlations and other distortion measures (see section 3.9) provide means of answering question (2). Answers to question (3) require either the "brute-force" randomisation approach (e.g. Harper 1978, Strauss 1982) or specific statistical tests, often with critical assumptions (e.g. Sneath 1977a, 1977b, 1977c, 1979a, 1979b). These tests commonly assume multivariate normality within groups and involve a multivariate extension of *t*-tests to test for group-overlap in multidimensional space. Sneath (1986) has developed a test for group multivariate-normality. Athough this approach is still under development, it is an area of considerable potential importance in answering the question which groups are valid statistically.

It is difficult to answer question (4) (how many groups should be recognised?) on mathematical grounds alone (Orford 1976). To answer it requires looking into the multidimensional space of the original data to see which groups are "real". This cannot be done directly. An indirect approach involves Andrews' (1972) multidimensional plots of individual objects, in this case taxa. The +/– data matrix can readily be transformed into quantitative co-ordinates within multidimensional space by means of Gower's (1967) principal co-ordinates analysis with an appropriate proximity measure. The co-ordinate scores for each object for all dimensions can then be mapped into a Fourier function and this transformation drawn from $-\pi$ to π. Each object is represented by a wave across the plot (e.g. Everitt 1978, Birks 1978). Taxa with similar distributions will have similar waves positioned close together. The partitioning results can be evaluated by means of these plots, and the number of useful groups with coherent patterns within them and of "rag-bag" objects with unique patterns can be decided (Everitt 1978).

Another potentially useful approach is to map out the distribution of elements for 2,3,4,... groups, and look for spatial coherence in the results, for example spatial autocorrelation for different partitioning levels (Wartenberg 1985). Wartenberg re-analysed the modern foraminifer data of Imbrie & Kipp (1971) who had considered 3 or 4 elements only. Spatial autocorrelation of the mapped groups show significant positive autocorrelations for 7 groups, implying 7 elements with geographically coherent patterns. This provides a guide to what elements warrant further interpretation. Ther is considerable potential for using other numerical techniques for spatial data analysis in quantitative biogeography (e.g. Cliff et al. 1975, Unwin 1981, Upton & Fingleton 1985).

3.11. Examples

Instructive and useful examples of the use of numerical partitioning techniques to delimit biotic elements include the analysis of British hepatics (Proctor 1967), ferns (Birks & Line unpublished), and ants (Baroni-Urbani & Collingwood 1976), European ferns (Birks 1976), Australian plants (Bridgewater 1976) and birds (Kikkawa & Pearse 1969), Indo-Australian birds, bats, and butterflies (Holloway & Jardine 1968, Holloway 1973), and Florida trees (Birks unpublished).

4. Numerical analysis of biotic affinities between geographical areas (Q-mode analysis)

Here the analysis is very similar to studying distributional affinities between taxa, except that now the analysis is Q-mode and the aim is to group the n areas on the basis of similar biotic composition. When the biotic regions are mapped, biogeographical regionalisation of the region of interest can be established (see Table 1 on page 172 for examples).

5. Future developments

There are at least four major areas where future developments could usefully take place.

5.1. Biogeographical regionalisation and comparison of classifications

With an increasing interest in quantitative descriptive biogeography and the compilation of large and comprehensive data-sets for different groups of organisms for the same region, it is important to compare biogeographical regionalisations based on different organisms, e.g. plants, birds, mammals, ants, and carabids in northern Europe. If comparable analyses (not necessarily using identical geographical

Table 1. Examples of biogeographical regionalisation based on numerical analysis of biotic affinities between areas.

Geographical area Taxonomic group	Author
British Isles	
Flowering plants	Birks & Deacon 1973
Hepatics & mosses	Proctor 1967
Ferns	Birks & Line unpub.
Bumblebees pre-1960	Williams 1982
Bumblebees post-1960	Williams 1982
Finland	
Birds	Järvinen & Väisänen 1980
Northern Europe	
Ants	Baroni-Urbani & Collingwood 1977
Europe	
Ferns	Birks 1976
Nematodes	Topham & Alphey 1985
Atlantic Ocean	
Seaweeds	Lawson 1978 van der Hoek 1975
Holarctic zone	
Psylloidea	Hodkinson 1980
Florida	
Trees	Birks unpub.
Indo-Australia	
Birds	Holloway & Jardine 1968
Bats	Holloway & Jardine 1968
Butterflies	Holloway & Jardine 1968
World	
Conifers	Sneath 1967 Birks unpub.
Red seaweeds	van der Hoek 1984 Joosten & van der Hoek 1984
Freshwater crustacea	Sneath & McKenzie 1973
Brachiopods	Waterhouse & Bonham-Carter 1975
Trilobites	Jell 1974
Insect pests	Ezcurra et al. 1978
Collembola	Blackith & Blackith 1975
Mammals	Smith 1983 Flessa 1981

areas but of a similar scale) existed for these groups, the regionalisation map for, say, ants could be gridded, and the regions recorded that particular grid points (ca. 200 total) lay in. The process is repeated for plants, birds, etc. The different geographical classifications can then be compared pair-wise and quantitatively using Rand's (1971) coefficient of agreement. The matrix of Rand coefficients (0 totally dissimilar, 1 identical) can be partitioned or ordinated numerically to detect similar and dissimilar classifications, the grouping of which may have interesting biological interpretations. A preliminary comparison of quantitative regionalisations of the British Isles for flowering plants, bryophytes, ferns, birds, ants, butterflies, and bumblebees indicates a major dichotomy between plant and animal regionalisation patterns, with the former having strong north-south *and* west-east gradients and the latter having marked north-south gradients only (Birks unpublished).

5.2. Development and use of spatially constrained partitionings

In analysing biogeographical data from continental land-areas, the geographical areas are not random, unconnected areas. They have a specific geographical location and geographical relationship with other areas. In view of this important geographical information, it is appropriate to impose some constraints on allowable groupings of areas based on their spatial relationships. This is relatively striaghtforward for linear geographical (e.g. McCoy et al. 1986, Webster 1980, Hawkins & ten Krooden 1979) and temporal gradients (e.g. Birks & Gordon 1985, Legendre et al. 1985). It is more difficult for two-dimensional geographical data. Deriving suitable algorithms for geographically constrained partitionings is currently an area of active research. Recent contributions include Perruchet (1979, 1983) and Gordon & Finden (1985). A review of existing approaches is.given by Gordon & Finden (1985). More research is needed, however, before there are robust and computationally feasible algorithms for spatially constrained partitioning that can analyse large biogeographical data sets.

5.3. Statistical developments

Much of what I have discussed above falls within Tukey's (1980) exploratory data analysis and Ball's (1975) descriptive phase in biogeography, and is designed to answer the question "what biogeographical regions or elements are there in the area of interest?" Hopefully, we can begin to answer the question Connor (1980) raised in reviewing Pielou (1979), namely "are there biogeographic regions"? Answers to this type of question require hypothesis testing and probabilistic statistics, and hence confirmatory data analysis. An appropriate null hypothesis is that there are no biotic regions (or elements) within the area of interest and that the observed similarities between regions (or taxa) do not differ from random expectation if the regions supported random, independent subsets of the "taxon pool" for the area as a whole.

Many existing proximity measures are non-statistical, sample-size dependent, and *ad hoc*. With the exception of the Jaccard and Baroni-Urbani & Buser coefficients, it is not possible, for example, to test for significant deviation from randomness for observed pair-wise comparisons (Simberloff et al. 1981, McCoy & Heck 1987). In comparing areas (Q-mode analysis), it is important to test whether observed similarities between areas do differ from expectation if the two areas had random and independent subsets of a "taxon pool" (Simberloff 1978, Connor & Simberloff 1978, Simberloff et al. 1981). By comparing observed number of taxa with expected number on the basis of random, independent subsets, Connor & Simberloff (1978) and Simberloff & Connor (1979) devised a useful probabilistic similarity measure for Q-mode analysis, along with its variance (Simberloff 1983) (see Wright & Biehl 1982 and Simberloff & Connor 1984 for further discussion and Raup & Crick 1979 for a related measure). Heck & McCoy (1987) discuss the Raup & Crick coefficient and illustrate problems in using it (and other related probabilistic coefficients) that arise from the difficulties of defining realistic taxon pools.

These measures can, after appropriate scaling, be used in numerical partitioning and non-metric scaling methods to analyse biotic similarities between islands in Scotland (Birks, Kerslake & Line unpublished). Raup & Crick (1979) and Crick (1980) display patterns within matrices of their probabilistic measures for echinoid distributions using non-metric scaling. Other biogeographical uses of these measures include McCoy et al. (1986) and McCoy & Heck (1987).

Independently, Wong and Hansell (1983) have incorporated a related probabilistic measure based on the hypergeometric distribution into a clustering method. Similarities between two objects fused together can only have variables consistent with a random, independent allocation model, and with a taxon pool explicitly defined for each cluster level. Within a given data-set not all objects may be grouped together because they are too dissimilar to fit a single-pool random model, suggesting that the data structure is not hierarchical and not consistent with a single taxon-pool (see Wong & Hansell 1983 for further details). This method has considerable potential in analytical biogeography.

Related attempts at deriving similarity measures with known probabilistic properties include Henderson & Heron (1977) and Grassle & Smith (1976). Approximate probability distributions for other coefficients can be derived by repeated randomisations (e.g. Rice & Belland 1982, Strauss 1982) and bootstrap and jackknife techniques (e.g. Smith et al. 1979, Smith 1985, Smith et al. 1986, Gilinsky & Bambach 1986). Useful introductions to the powerful techniques of randomisation, bootstrapping, and jackknifing include Edgington (1980), Efron (1975), Efron and Gong (1983), and Diaconis and Efron (1983). These techniques are designed to estimate standard errors of a test statistic or its probability distribution, and clearly have considerable potential for statistical developments in analytical and historical biogeography (e.g. Gilinsky & Bambach 1986, Connor 1986).

In the field of numerical classification, there is increasing interest and activity in the statistical evaluation of partitioning results — "it seems likely that the future will see further investigations of the links between classification and more formal statistical methodology. Such studies could provide a deeper understanding of the properties of various classification procedures and facilitate a more informed approach to the analysis of multivariate data" (Gordon 1981:53). A potentially important probabilistic partitioning technique for biogeographical data is Buser and Baroni-Urbani's (1982) method based on generalised homogeneity. The current state-of-the-art in numerical partitioning and its links with confirmatory and statistical data analysis is presented by Aldenderfer and Blashfield (1984) and Milligan and Cooper (1985). Linking statistical aspects of proximity measures and clustering (e.g. Wong & Hansell 1983) is clearly an area of great importance for future developments in analytical biogeography.

5.4. Data extraction and compilation

Although more and more atlases of distribution maps are being published, the extraction and compilation of distributional data in a form for numerical analysis remain a major problem. Nearly all such data are extracted manually. There is clearly great scope for automatic digitizing range limits and converting mapped distributions into +/– data for individual taxa from atlases (e.g. Beven et al. 1984, Connor 1987b).

Developments in text-reading hardware may even allow dot grid-maps to be read directly by machine.

6. Conclusions

It is important to remember that any numerical analysis can only be as good as the data on which it is based. Reliable and complete biogeographical data based on a sound, uniform taxonomy take many orders of magnitude more time to collect than it takes a computer to process the data. The biggest limitation in numerical biogeography at present is not a lack of computers or numerical techniques but a shortage of suitable data sets. Good biogeographical data are thus so valuable that any numerical analysis should be done critically using appropriate and robust quantitative techniques, such as those discussed above.

This raises the question of which methods, among the many now available, should be used. It is not possible to make any firm recommendations about which proximity measure, clustering criterion, or evaluation procedure to use. I do not believe that there is one all-purpose method that can be guaranteed to be appropriate with all data sets. Several bad methods have been proposed and used. Many methods are almost equivalent in some situations. What is recommended is that any numerical method used should be selected for its mathematical suitability to the biogeographical problem in hand and not simply used because a computer program or package implementing a particular method happens to be available. As more is discovered about the mathematical properties and inherent biases of particular numerical methods, it will hopefully become possible to select appropriate methods solely on theoretical criteria.

Experience indicates that if the patterns in a given data set are well-marked then they are usually detected by most methods with only minor differences in detail between methods. However, in some instances different numerical analyses of the same data can lead to very different conclusions and biological interpretations (e.g. Everitt 1980, Buckland & Anderson 1984, Birks & Gordon 1985). It is therefore important, in critical studies, to analyse the data using several methods. If the results agree, one can have some confidence in the reality of the biotic elements or regions proposed, as they are unlikely to be an artifact of the particular numerical method used. If the results do not agree, other approaches to exploratory data analysis such as scaling procedures and multivariate plottings should be used (e.g. Everitt 1978, Gordon 1981), and all partitioning and scaling results evaluated critically using randomisation procedures.

The early phase of numerical classification, particularly in numerical taxonomy and descriptive ecology, saw the proliferation of a huge number of partitioning algorithms (e.g. Cormack 1971), with little or no attention being paid to their biological assumptions or mathematical properties. In recent years, mathematicians have begun to study these techniques more critically and are attempting to relate their numerical properties to more formal statistical procedures (Gordon 1981). The adoption and critical use of these mathematical developments into quantitative biogeography is important and may help to unite the descriptive and analytical approaches in biogeography.

Acknowledgements. This paper is based on a lecture I gave at the Nordic Council of Ecology course on "Non-island biogeography" at Tvärminne in October 1986. I am particularly grateful to Yrjö Haila, Olli Järvinen, and Esa Ranta for making the course so stimulating and enjoyable; to them, Ed Connor, Ilkka Hanski, Rob Hengeveld, and all the other participants for many helpful comments and questions; to Hilary Birks and John Line for invaluable assistance; and to the Nordic Council of Ecology for supporting my participation at Tvärminne.

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Received 27.XII.1986
Printed 30.IX.1987