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Areas of Endemism: Definition and Recognition Criteria

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Methods of cladistic biogeography provide rigorous techniques for extracting the elements of common history within a biota (see Nelson and Platnick, 1981; Humphries and Parenti, 1986; Wiley, 1988; Brooks and McLennan, 1991). Although rigorous, the ability to apply these methods to real problems in biogeography is burdened by theoretical concerns with the delimitation of the units of analysis, areas of endemism. Henderson (1991) and Holloway (1992) noted that a major difficulty is the vague manner in which areas of endemism have been defined and that the criteria for identifying such areas have yet to be developed. Axelius (1991) concluded that some workers have been misled by imprecise statements regarding biogeographic methodology and attempted to clarify the identification of areas when distributions overlap.

Despite pleas in the literature for an extensive survey of distributional data, cladistic biogeographic methods are capable of giving a result (i.e., a hypothesis of area

interrelationships) regardless of the quality or quantity of data. Biogeographic analyses based on a single taxon and applying vicariance techniques are not uncommon (e.g., Bremer, 1992). These preliminary studies are important, but they cannot provide the evidence required to propose general hypotheses of area history. Incongruence poses difficulties at many analytical levels. We enumerate here some basic cases of distribution type and how we think areas of endemism should be defined for cladistic analysis. We emphasize the role that the subsequent addition of taxonomic groups plays in delimiting areas of endemism and the flexible nature of area delimitation. Delimited areas of endemism are hypotheses to be tested that can be modified in light of new data, much as non-monophyletic taxa can be redefined. We illustrate how this iterative technique can be applied to two commonly encountered situations and how delimitation of areas of endemism will be altered depending on the patterns observed.

The presence of at least one endemic species in each area under consideration is a requirement of the cladistic biogeographic model (Humphries and Parenti, 1986), but many authors do not recognize even this criterion (e.g., Axelius, 1991; Wallace et al., 1991). Unless at least one taxon from two monophyletic groups is endemic in an area, there can be no repeating pattern and therefore no a priori reason to expect a vicariance explanation for endemism over some other model. Platnick (1991) suggested that an area of endemism is, minimally, the "congruent distributional limits of two or more species," adding that "extensive sympatry at some scale must surely be a requirement." That is only the beginning of a practicable definition because it does not take into account phylogeny: areas of endemism are fundamentally historical entities, not distributional ones, and their definition should take history into account. General distributional congruence among taxa (e.g., Croizat, 1962) may suggest regions of concentrated endemism, but they are not necessarily relevant to delimiting areas for analysis. Distributional patterns are only sources of biogeographic information in the context of the relationships of the inhabiting organisms. The definition of an area based only on congruent distributions of taxa of unknown relationship can result in failure to distinguish composite areas, where endemism has two or more historical explanations (see Platnick and Nelson, 1984). Additionally, Platnick's (1991) definition is too restrictive in that it demands sympatry. The different ecological requirements of the diverse taxonomic groups that should be included in a cladistic biogeographic analysis preclude syntopy among species as a criterion identifying areas of endemism, and distributional fluctuations (e.g., range retraction) can, on a larger geographic scale, similarly preclude sympatry.

AREAS OF ENDEMISM: DEFINITION

We define an area of endemism as a geographic region comprising the distributions of two or more monophyletic taxa that exhibit a phylogenetic and distribu-

tional congruence and having their respective relatives occurring in other such-defined regions. This definition demands, minimally, a three-taxon statement for each group, with each taxon of each group occurring in an area of endemism.

There are two phases of research leading to the recognition of areas of endemism. The first is a basic taxonomic/distributional level of analysis in which the taxa are defined, their relationships hypothesized, and their distributions delimited. The second is a testing phase in which additional taxonomic groups (that have undergone the first phase) are incorporated into the analysis to identify possible areas of endemism and to test the historical reality of those areas. The first phase identifies and provides a cladogram of "areas of occurrence," or distributions, that are then tested in the second phase. Our "area of occurrence" is equivalent to the "area" defined by Humphries and Parenti (1986:93): a biogeographic region occupied by a monophyletic group of organisms or a species. It is not until the second phase has determined congruent phylogenies and congruent distributions (areas of occurrence) that areas of endemism are identified. The number of taxonomic groups considered might not be relevant to establishing areas of endemism in some instances because redundancy within a group might be caused by "missing taxa" that prevent recognition of additional clades with the same biogeographic histories (Parenti, 1991).

CRITERIA FOR RECOGNITION OF AREAS OF ENDEMISM

Partially Overlapping or Nested Areas

We use two hypothetical clades (I and II), each with three species (1-6), occurring in a set of four areas (A-D) to illustrate criteria for delimiting areas of endemism. One could visualize a continuum from two exclusive distributions to two congruent distributions with various amounts of overlap. Any amount of overlap suggests at least an initial hypothesis of historical commonality, in contrast to a notion of in-

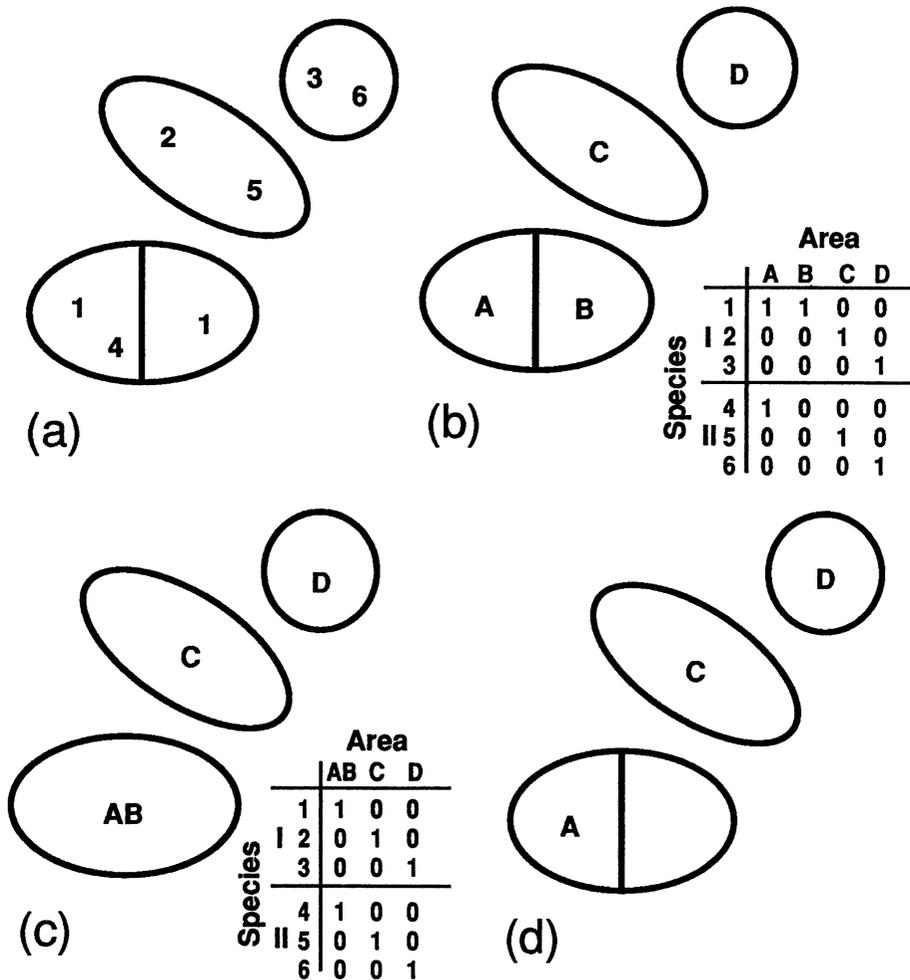


FIGURE 1. Delimitation of areas for biogeographic analysis from patterns of distribution. Four areas, A–D, inhabited by six hypothetical species in two clades: clade I (species 1–3) and clade II (species 4–6). (a) Patterns of distribution of six hypothetical species in two clades. (b) Four areas recognized, with species by area matrix. (c) Three areas recognized, species 1 and 4 endemic (species 4 epibiotic), with species by area matrix. (d) Three areas recognized, species 4 endemic, species 1 widespread; species by area matrix given in Figure 1b (minus area B). Recognition of an area B is not warranted given that it does not contain an endemic taxon. Area A may be an area of endemism, although the restricted range of species 4 might be a result of range retraction or habitat selection within a broader area AB. [Figures 1a and b modified from Axelius, 1991: fig. 1.]

dependence, and in the absence of information from other groups, only a single area can be recognized. This approach is contrary to that outlined by Axelius (1991), where the areas of overlap and the resultant remaining portions of the distributions are recognized as discrete areas (Figs. 1a, 1b). These recognized areas may, in some cases, not be defined by endemic taxa. Rather, area B (Fig. 1b) is defined by the

absence of taxon 4, and recognizing this area on the basis of a taxon occurring elsewhere is methodologically and philosophically unsound. Liebherr (1991) termed such portions of distributions paraphyletic areas and included them in an assessment of area relationships. A proposal of relationships among such areas is as meaningless as a classification of paraphyletic taxa.

There are two area classifications for the

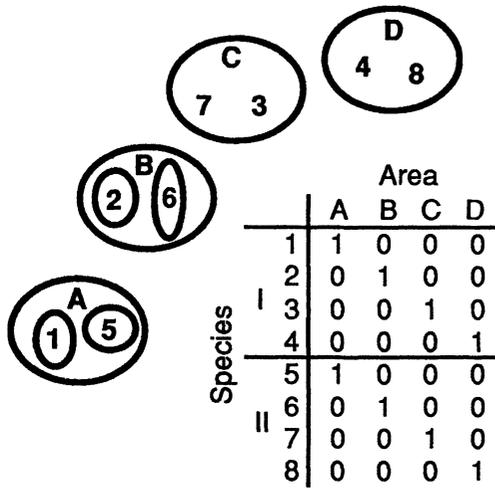


FIGURE 2. Four islands, A-D, inhabited by eight hypothetical species in two clades: clade I (species 1-4) and clade II (species 5-8). Distributional limit of each species is the shoreline of the island or a smaller ellipse. Area classification summarized in species by area matrix.

species distributions in Figure 1a that are worthy of consideration, each recognizing only three areas: a combined area AB plus areas C and D (Fig. 1c) or area A plus areas C and D (Fig. 1d). In Figure 1c, a combined area AB is formed based on two endemic species (species 1 and 4). In Figure 1d, species 4 is endemic to area A and species 1 is widespread. The data presented in this example allow us to distinguish between these two options: we select the interpretation that gives areas based on endemism with no areas stipulated by parts of species ranges (Fig. 1c as opposed to 1b or 1d). This classification utilizes all of the information available and does not include false areas (i.e., a separate area B).

There has been a bias in published analyses regarding the size of endemic distributions (e.g., Liebherr, 1991; Wallace et al., 1991), with the species distributions occupying the smallest geographic area being identified as endemics a priori, a practice without a well-developed basis in theory. The size of occupied areas resulting from a vicariance event will mainly be dependent on the way that the ancestral species ranges were subdivided by a barrier.

Nonoverlapping Distributions: Designation of Broad, Inclusive Areas

An area of endemism should be recognized on the basis of two or more endemic species being present, but contrary to theoretical treatments (e.g., Wiley, 1981; Platnick, 1991) their distributions do not have to overlap. Sympatry is not a requirement of cladistic biogeographic methods. By comparing the distributions and phylogenies of a diverse set of organisms, congruence is best explained by some common factor independent of the properties of the organisms themselves. At local and regional levels, the distributions of members of a diverse assemblage are not necessarily sympatric but they might be considered members of the same area of endemism.

A set of hypothetical islands and their inhabiting species (Fig. 2) illustrates this point. Two competing hypotheses of area relationships of the four islands are to be examined for compatibility with biogeographic data from clade I (species 1-4) and clade II (species 5-8). Two species inhabit each of islands A and B, but in both cases they are allopatric. At this level of analysis (among islands), the only reasonable set of areas and inhabiting taxa must be A (1, 5), B (2, 6), C (3, 7), and D (4, 8). In this instance, the boundary of the area of endemism must be expanded to encompass nonoverlapping species distributions. In a situation as described here, the likelihood of these defined areas being natural (not composite) will be tested as information from other groups of organisms enters the analysis (treatment of possibly composite areas was examined by Platnick and Nelson [1984] and Brooks and McLennan [1991]). Original area delimitations may also be falsified and replaced or modified. The important point is to provide a full account of how the areas of endemism have been defined and the limitations of these definitions (e.g., not testable with current data).

In so defining areas, the investigator may introduce information independent of biotic distribution; perhaps geological or physiographical features suggest that the area might be a single unit. For example,

three species occurring in different parts of a river basin can be considered members of the same area. It should be emphasized that discovery of composite origin is not prevented by this initial hypothesis of area. Ambiguity in the cladistic placement of this area of endemism should lead to a reexamination of area designation and recoding for the individual subareas. Platnick and Nelson (1984) treated this issue in some detail, providing an example based on New Zealand and its composite biota and geology.

If an investigator begins with a classification of areas that includes all of the small partial areas (local areas of endemism, in the terminology of Platnick and Nelson, 1984:329), any general relationships between the areas that these smaller partial areas comprise will remain undiscovered because these partial areas will be unique to some taxa in the analysis and will be considered uninformative.

Various studies have utilized broad area classifications (e.g., Andersen, 1991; Liebherr, 1991), but in many cases an ad hoc boundary was drawn to reach a compromise among incongruent patterns. This approach can result in the transformation of likely endemics into widespread taxa. Of even greater detriment, composite areas have in some instances been delimited for analysis by combining subareas without regard for phylogenetic patterns.

CONCLUSIONS

Platnick and Nelson (1984) emphasized the need for an abundance of data in performing biogeographic component analysis. Despite a growing library of cladograms, most investigators continue to restrict their analyses to their own specialty groups of organisms (e.g., Cracraft, 1986; Andersen, 1991; Griswold, 1991; Liebherr, 1991; Wallace et al., 1991). According to Nelson and Platnick (1981), the problem of area definition will disappear if a large number of diverse groups is examined: the historically meaningful areas will be indicated by co-occurring taxa. One of the major barriers to more inclusive studies is the inability to arrive at some

way of delimiting the units of analysis, areas of endemism. Therefore, the problems of historical biogeographic analysis are by no means restricted to arriving at a consensus or a parsimonious depiction of the data.

Widespread taxa present serious problems for biogeographic analysis (Nelson and Platnick, 1981). Their pervasiveness, though indicative of a low level of biogeographic information, does not interfere with obtaining a hypothesis of area relationships. One such example is the analysis of corals (*Acropora*) by Wallace et al. (1991), in which a fully resolved area cladogram resulted from a set of distributions in which only one of the four "areas" contained an endemic species. Our protocol would avoid such cases because areas of overlap, or even outlying or "paraphyletic" areas, can be recognized as parts of other areas. The identification of actual areas of endemism must await comparison with the distributions (and phylogenies) of other taxa and the discovery of two or more taxa sharing a distribution.

There is more to defining areas of endemism for analysis than merely looking for congruence of distribution. Most importantly, designated areas are hypotheses and as such are not indelible. Incongruence in the array of cladograms may be caused by ill-defined areas (e.g., the result of lack of endemism or composite origin) (Platnick and Nelson, 1984). Area delimitations should be reexamined, and the implications for the general area cladogram should be studied. This process is analogous to the testing of the homology of characters in phylogenetic analysis, but here we are testing the origins of species distributions. We contend that (1) overlapping distributions should be considered initially as elements of one area; subsequent testing can be performed using information from other taxonomic groups, a process that may lead to further subdivision of initial areas; and (2) nonoverlapping distributions need not be considered separate historical entities if there is independent evidence that the areas could be considered as one. Other information,

e.g., regional geology, can be used as an aid to defining areas of endemism for study, provided that these areas will contain some endemic taxa. Additionally, the relationships of the organisms themselves should be examined for the possibility of incongruence: this information can be used in deciding whether proximate forms are members of an equivalent area (see Parenti, 1991).

These contentions challenge current definitions and recognition criteria for areas of endemism. Because areas of endemism are the units of biogeographic analysis, it is imperative that biogeographers employ the same criteria for their determination if studies are to be comparable. If nothing else, workers must clearly present the evidence upon which their units of analysis are based. We present this discussion as an initial step in determining more formal criteria for improving the data collection for and, we hope, the results of cladistic biogeography.

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