

**Biogeography**--Why things are where they are.--

The field that attempts to document and understand the spatial patterns of organisms in the past and present and develop process explanations for variation in distribution.

I. Ecological Biogeography

- A. Typically deals with relatively recent patterns and interactions with an ecological and phenological emphasis.
  - 1. From this view questions addressed might be like "What allows a species to occur in one area and prevents it from expanding into other areas?"
- B. Community based.
- C. Can involve paleontological data, so is not restricted to currently extant populations.
- D. Studies often involve the impact of human activities; succession theory; the dynamics of communities and populations; fire ecology; restoration ecology; invasive species; species pulses or waves; island biogeography.

e.g., Elias, S.A., Berman, D., Alifimov, A. 2000. Late Pleistocene Beetle Faunas of Beringia: Where East meets West. *Journal of Biogeography*. 27:1349-1-63.

II. Phylogeography

- A. The attempt to take into account the geographic distribution of species/populations in establishing their phylogeny/divergence, and to understand the geographic patterns that may result from divergence, ultimately leading to speciation.
  - 1. Focus on species boundaries.
  - 2. Often looks at gene trees or genealogies.
  - 3. Shares methodology with phylogenetics.

e.g., Gody, J.A., Negro, J.J. Hiralodo, F., Donázar, J.A. 2004. Phylogeography, genetic structure and diversity in the endangered bearded vulture (*Gypaetus barbatus*, L.) as revealed by mitochondrial DNA. *Molecular Ecology*. 13:2 p. 371.

III. Historical Biogeography

- A. Usually involves older patterns inferred by looking at clades (often as species and higher taxa)
- B. Focus on why lineages are represented in certain areas and not others and why is a pattern of distributions frequently repeated in different lineages.
- C. Typically area relationships and general patterns of diversity are emphasized over single taxon distributions.

e.g., Marshall, C. J., Liebherr, J.K. 2000. Cladistic biogeography of the Mexican transition zone. *Journal of Biogeography*. 27( 1):203-216.

IV. Brief Historical overview of "periods" and discoveries

- A. At the time of a limited view of dynamics and diversity
  - 1. Creation myths, dispersal from Noah's ark, etc.
  - 2. Little understanding beyond local flora/fauna
- B. Age of exploration
  - 1. 17th century led to discovery of too many species for the Ark
  - 2. Realization that environmentally similar but distantly isolated regions have distinct assemblages of organisms (Buffon's Law)
  - 3. Islands have lower diversity
  - 4. Similar floristic zonation (Humbolt)
- C. 19th century, advances in geology and evolutionary theory
  - 1. Lyell, Darwin, Wallace, Sclater, Hooker, etc.
  - 2. Abandonment (by most) of the idea of static distribution and immutability of species.

3. Landbridges/megacontinents (e.g. Hooker, Wallace) vs. dispersal (e.g. Darwin)

D. 20<sup>th</sup> century

1. Continental drift (Wegener 1912)- but not really accepted until 1960s- (Dietz & Holder 1966) Persistent dispersalists like Mayr and Darlington maintained that even if continents moved dispersal was still more important.
2. -Panbiogeography of Croizat, phylogenetics of Hennig and implementation Brundin (1966) for a trans-Gondwanan group of flies
3. Vicariance biogeography fully developed by Platnick & Nelson (1978)

V. Generally used current methods of Historical (Vicariance) Biogeography

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-Similar systems like parasites and their hosts can use the same or similar methods.

Host -- Associate

organism -- paralogous gene

host organism - parasite organism

geographic area - organism

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- A. Historical explanation for disjunct patterns can be either dispersal or fragmentation of a continuous range (vicariant).
- B. Vicariance biogeography usually considers dispersal to be an ad hoc explanation that could be used to account for any pattern.
- C. Implied process assumptions in pattern methods, which are more explicit in event-based methods
  1. allopatric speciation is relative more common
  2. dispersal is relatively less common than stasis
  3. current distributions generally reflect ancient events

D. The basics

1. You need monophyletic groups that occur in three or more areas
  - a. Requires that you assume the phylogeny is correct
2. Replace the OTU names with area names to make taxon-area cladograms
  - a. Requires you assume the known ranges are adequate
3. Summarize the set of taxon-area cladograms to make a general area cladogram that shows the congruent vicariant pattern
  - a. Assumption of simplicity or at least that the majority of taxa respond the same most of the time
4. "Missing", widespread taxa and redundant areas are problems.
  - a. Areas may be absent in groups because
    - i. no member ever occur in the area
    - ii. sampling error
    - iii. extinction
  - b. Taxa may occur in more than one area because
    - i. non-response to a vicariant event
    - ii. sympatric speciation
    - iii. dispersal (secondary sympatry)
3. Redundant distributions in two taxa
  - i. dispersal in one or both taxa

VI. *A priori* methods- Derive general biogeographic patterns from shared cladistic patterns and distributional data. No secondary or "total evidence" analysis.

A. Component Analysis. TAC, FAC, RAC, GAC: Use taxon area cladograms (TAC) to derive reduced area cladograms (sometimes called fundamental area cladograms (FAC)) from phylogenetic hypotheses and distributional data under Assumptions 0, 1, 2 (Platnick & Nelson 1978). General Area cladograms (GAC) are the intersection of reduced area cladograms (RAC) from two or more sets of trees.

**Assumption 0:** assumes that widespread taxa are the result of non-response to only the most recent vicariant event (can we know if this was not a dispersal event?), so that areas that are occupied by widespread taxa are interpreted as being most closely related. Clearly, the existence of more than one widespread taxon, each occupying overlapping but not identical sets of areas are conflicting evidence for area relationships. The conflict is resolved for these redundant areas for the most apical cladistic position.

**Assumption 1:** assumes that widespread taxa are the result of non-response to the most recent OR earlier vicariant event (dispersal event?). Redundant area representations are all considered valid. The assumption will often produce more trees (the convex set) than the more restrictive assumption 0, but will always include Assumption 0 trees as a subset.

**Assumption 2:** allows for the possibility that dispersal, as well as non-response to a vicariant event, may be the explanation for widespread taxa. (fix one move the other to all possible positions).

B. Reconciled Trees (Page 1990, 1994): Mapping one tree onto another by the inclusion of unobserved events.

1. User tree (host or area relationships) mapped to observed or associate tree (taxa or parasites)
2. Items of Error (IOE): Mis-fit of the trees. Number of nodes in reconciled tree – number of nodes in associate tree (in Component 2.0 "leaves added" =  $\frac{1}{2}$  IOE)
3. Various area cladograms are reconciled to find an optimal fit.
4. Heuristic searches may focus on trees that minimizes leaves added, however this may overestimate the number of events.

C. We have been using "areas" but what are Areas of Endemism?

1. "if they are not exactly congruent, but are largely congruent, then they may be considered equivalent for purposes of biogeographical analysis." (Wiley 1981 )
2. What the terminals are in a biogeographic study is fundamental to doing the analysis in the first place. However, there has been much less attention given to area definition/discovery than to tree conversion/combination in to a general area cladogram. An Area of Endemism is an area of nonrandom distributional congruence. (Morrone 1994).
3. Most frequently AofE are determined intuitively through inspection of distributional information and often endemic areas are equivalent to species distributions. However, various grid methods have been used (Morrone 1994; Linder 2001; Szumik et al. 2002, all in Sys. Bio).
4. Linder (2001) published these criteria:
  - i. The ranges of the species endemic to the area of endemism should be maximally congruent. Ideally all taxa would be evenly distributed in the area. [generally not the case ]
  - ii. The areas of endemism should be narrower than the whole study area, so that several areas are located.
  - iii. Areas of endemism must be mutually exclusive, and grid squares (or any other units) cannot belong to two areas of endemism.
  - iv. If areas of endemism are to be determined before cladistic biogeographical analysis, then that definition should not be open to retrospective modification, which this would weaken the power of incongruent distributions in falsifying any patterns.
5. A simple example using PAE (parsimony analysis of endemism, Rosen 1988; Morrone 1994)

- i. Draw quadrats (grid) on a map, consider quadrats only where at least one locality record exists for a study taxon.
- ii. Construct a data matrix where columns are species and rows are quadrants. Use 0-1 = absence - presence coding.
- iii. Add an all zero quadrant (the empty or what we might call the Stanford quadrat) as a hypothetical root (where nothing exists).
- iv. Analyze for the parsimony solution.
- v. Delimit groups of quadrats with at least two species
- vi. Superimpose the delimited groups on the map to delineate the AofE boundaries.