April 24, 2020. **Biogeography III: spatial phylogenetics, including phylobetadiversity & biome recognition, and other spatial issues**

Spatial phylogenetics is a relatively new field that takes a "big-data" approach integrating large-scale phylogenies with spatial and environmental data to study biodiversity in an evolutionary context. It represents a new area of biogeography that synthesizes historical and ecological biogeography. See also separate file with figures.

1. Phylogenetic alpha diversity

Biodiversity is usually measured by examining changes in the pattern of species distribution across a region to identify areas of particularly high diversity and endemism. Beta-diversity, or turn-over on the landscape, is likewise usually measured by comparing proportions of species shared among areas. However, investigations based on species distributions alone miss the full richness of analyses that can result from taking a phylogenetic approach. Hotspots of diversity and endemism can be mapped, their make-up assessed, and similarities and differences among them characterized. Using hypotheses tests based on spatial randomization, insights can be gained into ecological, evolutionary, and biogeographic processes that have shaped these patterns.

The phylogenetic diversity metric (**PD**) was pioneered by Faith (1992); it is the amount of an overarching phylogeny that is present in a location. Phylogenetic endemism (**PE**) was proposed by Rosauer et at. (2009); it is also the amount of an overarching phylogeny that is present in a location, but where the phylogenetic branch lengths have been weighted by their geographic ranges such that small-ranged branches contribute more, while wide-ranged branches contribute less.

Relative Phylogenetic Diversity (**RPD**) and Relative Phylogenetic Endemism (**RPE**) are related metrics; both are ratios that respectively compare PD or PE measured on the original phylogeny against the PD or PE measured on a comparison phylogeny that has the same topology but with all branches adjusted to be of equal length (Mishler et al., 2014). RPD and RPE are designed to detect concentrations of unusually short or long branches on the map.

These phylodiversity metrics are all rank-free since it does not matter what taxonomic levels the terminals represent, as long as they are monophyletic and their geographic distribution can be characterized, and are thus relatively robust to lumping and splitting decisions by taxonomists.

2. A range-weighted tree

To fully understand PE, and other methods discussed below, it is important to introduce the concept of a *range-weighted tree* (**RWT**). To generate a RWT, one starts with a phylogenetic tree including branch lengths and divides the length of each branch by its range size. The range of a non-terminal branch in a tree is taken to be the union of the ranges of descendants of that branch. The RWT thus keeps the topology of the original tree, but the branch lengths are adjusted such that the wider-ranging branches are disproportionately shrunken down and most of the length of the tree is in range-restricted branches. The RWT is extremely useful in several contexts. For one thing, it is the basis for PE: PE can be most simply understood as PD measured on a RWT.

One use of range-weighted trees is in Categorical Analysis of Neo- And Paleo-Endemism (**CANAPE**) is a two-step method that employs a spatial randomization to allow for the first time a clear, quantitative distinction between centers of neo- and paleo-endemism across a region (Mishler et al. 2014). Step one of CANAPE is to establish that a location is a center of high PE: it must be significantly high (one-tailed test) on either the RW original tree, the RW comparison tree or both. Step two is to examine the significance of the RPE ratio itself (two-tailed test). If the ratio is significantly high, that means the range-restricted branches in that location are longer than expected (indicating a concentration of paleo-endemism). If it is significantly low, that means the range-restricted branches in that locality are shorter than expected (indicating a concentration of neo-endemism). When the ratio is neither significantly high nor low, Mishler et al. (2014) called such locations a concentration of "mixed endemism," the interpretation being that there is some unknown mixture of lengths of range-restricted branches in that location that is not dominated by either neo-endemism or paleo-endemism.

3. Phylogenetic beta-diversity

Biodiversity is conventionally partitioned into three levels: alpha, beta, and gamma. Gamma diversity is the total diversity across a study region, alpha diversity is the local diversity within subsets of that region, while beta diversity is the degree of compositional change, or turnover, of diversity between subsets. As described in Graham and Fine (2008), many ecological and evolutionary processes can be addressed by examining patterns of phylogenetic beta-diversity: community phylogenetics, spatial and taxonomic scaling issues, mapping ecological and habitat traits onto phylogenies, contrasting species beta diversity with phylogenetic beta diversity, etc.

Typical measures for comparing locations for biodiversity look at partitioning of species composition, measured via a dissimilarity index such as:

$$\text{Jaccard} = 1 - \frac{A}{A+B+C} \qquad \text{Sorensen} = 1 - \frac{2A}{2A+B+C}$$

Where A is the count of species found in both neighbor sets, B is the count unique to neighbor set 1, and C is the count unique to neighbor set 2.

There is an exact phylogenetic analog of these indices: Phylo-Jaccard and Phylo-Sorensen, where A is the length of shared branches, and B and C are the length of branches found only in neighbor sets 1 and 2, respectively.

A pairwise dissimilarity matrix in one of these measures, comparing all grid cells with all other grid cells, can be used as the basis for a cluster analysis such as UPGMA (Biodiverse software). Examining the similarity of grid cells is useful for many purposes as described below.

4. Range-weighted turnover metrics

Range-weighted trees are useful in measuring turnover on maps. Phylogenetic beta-diversity is normally measured by comparing the branches of a phylogenetic tree that are shared and not shared between two locations (Graham & Fine, 2008). A new type of phylogenetic beta-diversity measure was recently proposed by Laffan et al. (2016): range-weighted phylogenetic turnover (PhyloRWT). PhyloRWT examines turnover in amount of the RWT shared among locations, differing from conventional phylogenetic measures by emphasizing the branches that are range-restricted. It is equivalent to PE turnover. It serves as a particularly useful measure of phylogenetic beta-diversity for purposes of detecting boundaries of centers of endemism or biotic regions on the landscape, which may be obscured by widespread taxa when using conventional measures. PhyloRWT can be applied for a variety of purposes including bioregionalization, ecological studies of causes for beta-diversity, and complementarity analyses for applied conservation planning studies.

5. Biome recognition

One area of biogeographic research that can be greatly enhanced using this new phylogenetic approach is the recognition of biomes, or biotic regions. This area has a long and proud tradition -- most parts of the world have vegetation maps, or faunal maps, or combined biotic maps. These have traditionally been based on a intuitive line-drawing process taking into account distributions of biological taxa and/or geologic, soil, or climatic factors. However, biome boundaries are better based on objective turnover measures of shared species or shared branches (González-Orozco et al., 2014).

6. References

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