April 25, 2014. Biogeography III: Finding centers of endemism, measuring phylogenetic beta-diversity, biome recognition, and phylogenetic niche modeling

This seemingly diverse set of topics is united by the shared goal of using phylogenetic information to understand large-scale patterns on the landscape of taxon ranges in relation to ecological and evolutionary processes. Methods are developing rapidly, as are sources of distributional and environmental data. A brand-new area of biogeography is being borne, synthesizing historical and ecological biogeography.

Centers of endemism

Building on the lecture 4/18/14 on conservation and phylogenetics, locations (i.e., grid cells) of high phylogenetic endemism can be found using the PE and RPE metrics, along with the CANAPE (Categorical Analysis of Neo- And Paleo-Endemism) randomization. How can we group these grids cells into centers of endemism?

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

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

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

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 can lead to an objective grouping (classification) of grid cells into centers of endemism -- and for many other purposes as described below.

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 the Graham and Fine article (2008, *Ecology Letters*, 11, 1265-1277), 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.

Range-weighted turnover metrics

Turnover measures (e.g., Jaccard and Sorensen), are all based on a partitioning of the alpha diversity of the combined sites. This means that, since measures of endemism are also alpha diversity metrics, range-weighted turnover metrics can be calculated as a direct modification of established range restriction metrics. We should use PE as the metric of comparison for addressing some types of questions (unpublished manuscript entitled "Range-weighted metrics of species and phylogenetic turnover" by Laffan, Rosauer, Mishler, Miller, González-Orozco, & Knerr).

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. Phylogenetic turnover metrics can be used to draw these lines objectively (C. E. González-Orozco, M.C. Ebach, S. Laffan, A.H. Thornhill, N.J. Knerr, A.N. Schmidt-Lebuhn, C.C. Cargill, M. Clements, N.S. Nagalingum, B.D. Mishler, and J.T. Miller. 2014. Quantifying phytogeographical regions of Australia using geospatial turnover in species composition. PLoS ONE 9(3): e92558).

Phylogenetic niche modeling

"Environmental niche" usually refers to what conditions a *species* requires to maintain its populations. The Grinellian niche involves the set of environmental variables that shape the taxon distribution, whereas the Eltonian niche focuses on the dynamics of biotic interactions with other organisms (Grinnell 1917). Hutchinson (1957) proposed the combination of the Grinellian and Eltonian concepts to create a global niche concept -- Hutchinson's concept treats the Grinellian niche as the "fundamental niche" and the Eltonian niche as the "realized niche."

To explore how the niche varies in space and time it is necessary to investigate niche dynamics through evolution. Phylogenetic niche conservatism has been studied by a number of authors (e. g., Wiens & Graham 2005; Losos, 2008; Prinzing et al. 2011). Ecological divergence may intimately follow phylogeny if closely related species share similar ecological requirements. Studies to date that have included phylogeny in the study of ecological niches (Yesson & Culham 2006; Warren et al. 2008; Evans et al. 2009; Smith & Donoghue 2010; Waltari et al. 2011; Liu et al. 2012) have used ancestral reconstruction (AR) techniques to infer environmental preferences for ancestral nodes

Can we develop a less speciesist way to define and study niches? Why can't a clade at any level, above or below the named species level, have a niche? A different and perhaps better approach to integrate phylogeny with studies of ecological niche evolution could be called Phylogenetic Niche Modeling (PhyNM). Specifically, this approach directly models the niches of all nodes in the phylogeny, instead of the ancestral reconstruction approach that models only the species, uses phylogenetic methods to get nodal values, and then uses these results to infer niche evolution. The jury is still out on the differences between PhyNM and AR, more work is needed, but this is an exciting area for future development (unpublished manuscript entitled "Phylogenetic Niche Modeling: a case study with Australian hornworts" by González-Orozco, Mishler, Knerr, Cargill, Thornhill & Miller).

References for last section

Evans ME, Smith SA, Flynn RS, Donoghue MJ (2009) Climate, niche evolution, and diversification of the "bird-cage" Evening Primroses (Oenothera, Sections Anogra and Kleinia). The American Naturalist, 173, 225-240.

Grinnell J (1917) The niche-relationship of the California thrasher. Auk 34, 427-433.

Hutchinson GE (1957) Concluding remarks. Cold spring Harbor Symp, 22, 415-427.

Losos, JB (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecological Letters, 11, 995-1003.

Liu H, Edwards E, Freckleton RP, Osborne CP (2012) Phylogenetic niche conservatism in C4 grasses. Oecologia DOI 10.1007/s00442-012-2337-5

Prinzing A, Durka W, Klotz S, Brandl R (2001) The niche of higher plants: evidence for phylogenetic conservatism. Proceedings of the Royal Society of London B, 268, 2383-2389.

Smith SA, Donoghue J. M (2010) Combining historical biogeography with niche modelling in the caprifolium clade of Lonicera (Caprifolicaceae, Dispsacales). Systematics Biology, 59, 322-341.

Wiens JJ, Graham CH (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology, Evolution and Systematics, 36, 519–539.

Waltari E, Hijmans RJ, Peterson AT, Nyari AS et al. (2011) Locating Pleistocene refugia: Comparing phylogeographic and ecological niche model predictions. PLos ONE, 7, 1-11.

Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution, 62, 2868-2883.

Yesson C, Culham A (2006) Phyloclimatic modelling: combining phylogenetics and bioclimatic modelling. Systematics Biology 55, 785-802.