

Nice weather for frogs – using environmental data to model phylogenetic turnover

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1. Overview

This paper describes a new technique, generalised dissimilarity modelling of phylogenetic diversity, and its application to mapping phylogenetic differentiation in Australia's hylid frogs.

1.1 The biodiversity mapping problem

Mapping the distribution of elements of biodiversity is essential to any planned approach for allocating resources to conservation, as well as to understand macro scale evolutionary processes.

For well studied areas, 'point' data from observed locations of each species may provide sufficient information. For well studied species, a range of modelling techniques are available to extrapolate from known locations, using climate and other environmental data to predict areas of suitable habitat for the species. But these approaches have limitations for broad scale applications such as conservation planning, where we may need to consider all species and areas, including those for which data are sparse.

1.2 Generalised dissimilarity modelling

The generalised dissimilarity modelling (GDM) approach (Ferrier *et al.*, 2004, 2007) handles these problems by modelling not individual species or communities, but an emergent property of biodiversity, beta diversity, which is the difference between the assemblage of species found at any two sites. Beta diversity, or species turnover, can be represented as a biological distance between a pair of sites using a distance measure such as the Bray-Curtis dissimilarity index which gives a value ranging from 0 (same species found at both sites) to 1 (no species shared between the sites). GDM relates biological distance to distance in environmental space, and allows for a non-linear relationship between biological distance and distance in each environmental variable. The resulting model uses transformed environmental distances to predict the biological distance between locations, and thus to represent the overall spatial pattern of compositional turnover across the study area.

Applications of the GDM approach include conservation assessment, constrained environmental classification, survey gap analysis, and climate-change impact

assessment (Ferrier *et al.*, 2007, p252). It has also been shown to be one of the most effective techniques for species distributional modelling (Elith *et al.*, 2006).

2. Phylogenetic GDM

A novel addition to the GDM method is to model biological distance based on phylogenetic beta diversity rather than species beta diversity.

2.1 Phylogenetic beta diversity

Phylogenetic beta diversity (Graham and Fine, 2008) is analogous to species beta diversity, except that the units shared between sites are not species, but branches on the phylogeny, representing units of evolutionary history. There are many advantages of this approach to biological distance (see Graham and Fine, 2008), but importantly for GDM, the measure responds to differences in the composition between sites even where no species are shared, giving a far broader range of distance measurement. For example, as composition changes along an environmental gradient, a species may be replaced by close relatives, and this is reflected by a phylogenetic distance measure. Here, phylogenetic beta diversity is calculated using a modified form of Sørensen or Bray-Curtis distance:

$$d_{ij} = 1 - \frac{2A}{2A + B + C} \quad (1)$$

where A is the length of the branches common to both sites, i and j ; B is the length of the branches present only at site i ; and C is the length of the branches present only at site j . A branch is present at a site if it is on the path linking the taxa at the site to the root of the phylogenetic tree (Faith, 1992). As illustrated in fig. 1, two sites may share no species, but still have a biological distance less than 1, if they share common ancestors within the phylogeny used for analysis.

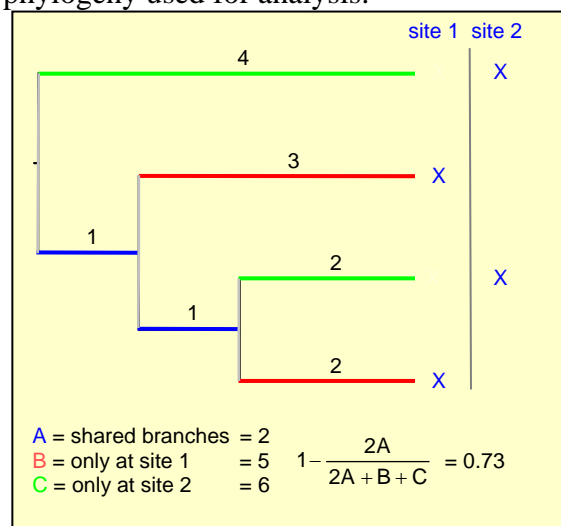


Figure 1. Calculating phylogenetic beta diversity between two sites. In this example, two sites share no species, so the species-based Bray-Curtis distance is 1, while the phylogenetic distance reflects the degree to which the species are related to each other.

2.2 Creating a phylogenetic generalised dissimilarity model

Ferrier *et al.* (2007) proposed a method for using GDM with phylogenetic distances, and Graham & Fine (2008) recently argued the benefits of this approach to “evaluate

what types of environmental gradients or barriers influence turnover for different species groups” (p1272). Such a method has not yet been implemented, so this study set out to do so.

Georeferenced specimen and survey records for Australian frogs in the family Hylidae were compiled from Australian Museums and selected government agencies to form a set of 90,800 location records for 78 species. Locations were rounded to the nearest 0.01 degrees, with each location at this precision treated as a site. Species recorded at the resulting sites were linked to a molecular phylogeny for the Australo-Papuan hylid frogs generated by Steve Donnellan (Rosauer *et al.*, in press). A table of phylogenetic distances between site pairs was calculated according to the phylogenetic beta diversity method described above, using a custom built extension to the Biodiverse software package (Laffan *et al.*, 2008).

Environmental data for the model comprised grids at 0.01 degree resolution including the full range of 35 ANUCLIM interpolated climate surfaces (Houlder *et al.*, 2000), as well as indices of topography and drainage.

The GDM model was generated using Generalised Dissimilarity Modeller (Manion, 2009) which implements the model fitting methods described by Ferrier *et al.* (2007). The table of phylogenetic distances for site pairs generated using Biodiverse provided the biological input to the model. An unsupervised nearest neighbour classification grouped pixels into 50 classes.

2.2 Results of a phylogenetic generalised dissimilarity model

The resulting GDM explained 33% of the variance in phylogenetic distance between site pairs. Of the environment variables used, 18 were selected to contribute to the model, and the most important in order of contribution were: precipitation of the wettest quarter, mean temperature of the wettest quarter, radiation seasonality and mean temperature of the warmest quarter.

A classification based on the phylogenetic distances predicted by the GDM indicates the broad patterns of phylogeographic structure for Australia’s tree frogs (fig. 2), such as the strong differentiation and narrow extent of classes in the Wet Tropics, a centre of endemism and strong phylogenetic differentiation for hylid frogs (Rosauer *et al.*, in press). The broad classes across inland Australia reflect the fact that this area is dominated by very widespread species of the genus *Cyclorana* across shallow environmental gradients.

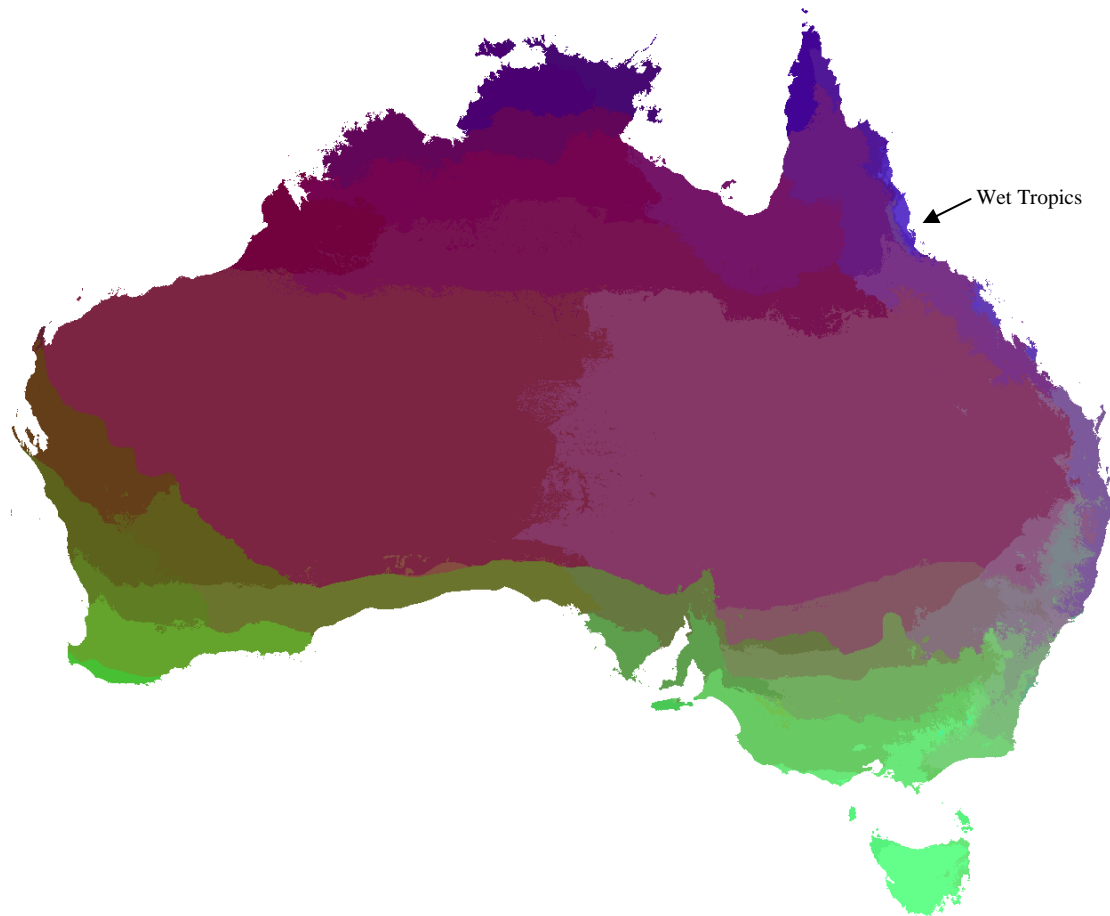


Figure 2. Classification by predicted phylogenetic distance for hylid frogs. Similar colours indicate shared or closely related species.

Further work will refine and test the phylogenetic GDM technique and develop its application to questions of biogeography and conservation priorities.

3. Acknowledgements

Thanks to Janet Stein for preparing the environmental grids used in this project. The Australian museum and CSIRO faunal collections provided specimen records. Dan Rosauer was hosted by the CSIRO Centre for Plant Biodiversity Research and as a visiting fellow at the Centre for Macroevolution and Macroecology in the Research School of Biology, Australian National University. This work was supported by an ARC linkage grant, a Caring for Our Country Grant and by the Department of the Environment, Water, Heritage and the Arts.

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