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# Phylogenetic generalised dissimilarity modelling: a new approach to analysing and predicting spatial turnover in the phylogenetic composition of communities

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Compared to species turnover, patterns of phylogenetic turnover provide extra information about the spatial structure of biodiversity, for example providing more informative comparisons between the biota of sites which share no species. To harness this information for broad-scale spatial analysis, we present phylo-GDM, a technique for interpolating the spatial structure of phylogenetic turnover between sampled locations in relation to environment, based on generalised dissimilarity modelling (GDM).

Using a database of over 150 000 location records for 114 myobatrachid frog species in Australia, linked to a species-level phylogeny inferred from 2467 base pairs of mitochondrial DNA, we calculated species and phylogenetic turnover between pairs of sites. We show how phylogenetic turnover extended the range of informative comparison of compositional turnover to more biologically and environmentally dissimilar sites. We generated GDM models which predict species and phylogenetic turnover across Australia, and tested the fit of models for different ages within the phylogeny to find the phylogenetic tree depth at which the relationship to current day environment is greatest. We also incorporated explanatory variables based on biogeographic patterns, to represent broad-scale turnover resulting from divergent evolutionary histories. We found that while the predictive power of our models was lower for full phylogenetic turnover than for species turnover, models based on the more recent components of the phylogeny (closer to the tips) outperformed species models and full phylogenetic models.

Phylo-GDM has considerable potential as a method for incorporating phylogenetic relationships into biodiversity analyses in ways not previously possible. Because phylogenies do not require named taxa, phylo-GDM may also provide a means of including lineages with poorly resolved taxonomy (e.g. from metagenomic sequencing) into biodiversity planning and phylogeographic analysis.

Generalised dissimilarity modelling (GDM, Ferrier 2002, Ferrier et al. 2004, 2007) is a statistical technique for modelling turnover in species composition between assemblages at sampled locations as a function of environmental and geographical attributes. Such models have proven useful for application to problems in biodiversity conservation involving spatial analysis across large numbers of species, such as assessment of land-cover change impacts (Allnutt et al. 2008), climate-change vulnerability analysis (Mokany et al. 2012, Prober et al. 2012), biological survey planning (Funk et al. 2005, Ashcroft et al. 2010), conservation prioritisation (Ferrier et al. 2004, Leathwick et al. 2010) and reserve gap analysis (Ferrier et al. 2004). Recently, GDM has been applied to model evolutionary relationships in various ways, including to predict similarity of invertebrate assemblages from phylogenetic dissimilarity of host species (Nipperess et al. 2012, see also Krasnov et al. 2010), to model the spatial structure of genetic or morphological variation within species (Freedman et al. 2010, Thomassen et al. 2010, 2011, Smith et al. 2011) and to explain between site differences in hybridization (Carling and Thomassen 2012).

When Ferrier et al. (2007) formally described GDM, they proposed an extension to model spatial patterns of phylogenetic turnover to generate a predictive model of phylogenetic beta diversity. Such a technique for modelling turnover in phylogenetic composition has many potential uses, but to our knowledge, has not been applied. Here we present a first implementation of this approach.

Because our study uses both species and phylogenetic measures of turnover in the same modelling framework, we sought a generic term for the difference between the

biota of two sites. The term 'composition' has been used to refer to species, phylogenetic and even functional composition (Swenson 2011, Swenson et al. 2012). Following this usage we use compositional turnover to refer to difference between assemblages in species or phylogenetic composition, or intermediate metrics (Methods). Where required, we refer to species or phylogenetic turnover in particular.

## Modelling phylogenetic turnover

GDM normally works with a measure of compositional turnover derived directly from the lists of biological entities (typically species) recorded at each of two sites – for example, the Sørensen dissimilarity index (Sørensen 1948, Bray and Curtis 1957), which gives a value ranging from 0 (same species found at both sites) to 1 (no species shared between the sites). GDM uses data on species observed at sampled sites to fit a model predicting the compositional dissimilarity between any given pair of sites as a multivariate non-linear function of differences in the environmental attributes, and optionally of the geographical separation, of these sites. This is formulated as a generalised linear model, with a link function addressing the asymptotic relationship between the ecological distance $\eta$ separating a given pair of sites, and the compositional dissimilarity $\mu$ between these sites:

$$\mu = 1 - c^{-\eta} \quad (1)$$

where $\eta$ is the sum of absolute differences between the two sites, $i$ and $j$, for a set of non-linear functions fitted to $n$ environmental attributes ($x_1$ to $x_n$):

$$\eta = \alpha + \sum_{p=1}^{n} \left| f_p(x_{pi}) - f_p(x_{pj}) \right| \quad (2)$$

and where the functions $f(x)$ in this equation are fitted as monotonic I-splines (Ferrier et al. 2007).

While this standard GDM approach – 'species GDM' – has proved useful for the analysis of multi-species spatial structure, it is limited in one key respect. As one compares sites along an environmental gradient, species compositional dissimilarity (e.g. the Sørensen index) generally increases with increasing difference in environment. Once no species are shared, however, the Sørensen index (like other species-based dissimilarity indices) becomes saturated, and no further increase in dissimilarity can be represented (Stegen and Hurlbert 2011). This has important implications for analyses based on this type of index. Consider for example a site in a rainforest. It has a species dissimilarity of 1 from another rainforest site with distinct but closely related species, but also has a species dissimilarity of 1 to a desert site with which it has no compositional overlap up to family level (Graham and Fine 2008). So these differences are represented as equivalent, and a whole spectrum of biological variation beyond the level of shared species is missed by such indices of species turnover (Ives and Helmus 2010).

A solution may be found in a phylogenetic implementation of the Sørensen dissimilarity which Ferrier et al. (2007) described, and proposed for use with GDM. Similar measures of the phylogenetic overlap between two samples or communities, have been used recently under a range of names including UniFrac (Lozupone and Knight 2005), PhyloSor (Bryant et al. 2008), and phylogenetic diversity (PD) dissimilarity (Faith et al. 2009). These measures are analogous to Sørensen dissimilarity, except that the units shared between sites are not species but rather lengths of branches on the phylogeny representing units of evolutionary history in common (Ferrier et al. 2007).

The Sørensen indices of species turnover ($Sør_{species}$) and phylogenetic turnover ($Sør_{phylo}$) between two sites ($i$ and $j$) are both calculated as:

$$1 - \frac{2A}{2A + B + C} \quad (3)$$

For $Sør_{species}$, $A$ is the number of species found at both sites $i$ and $j$; $B$ and $C$ are the numbers of species present only at site $i$, or site $j$ respectively. For $Sør_{phylo,}$ $A$ is the summed length of the branches common to lineages found at both sites $i$ and $j$; $B$ is the summed length of the branches present only at site $i$; and $C$ is the length of the branches present only at site $j$. Following the method for phylogenetic diversity (PD) (Faith 1992), 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, Moritz and Faith 1998). These Sørensen measures range from 0 (identical composition) to 1 (no shared branches or species).

Several recent studies have applied measures of phylogenetic turnover to quantify phylogeographic structure along environmental gradients (Bryant et al. 2008, Faith et al. 2009, Graham et al. 2009, Thomassen et al. 2010). For example, Bryant et al. (2008) found that phylogenetic turnover for soil *Acidobacteria* along an elevation gradient was greater than would be expected from the level of species turnover, suggesting that deeper lineages as well as species were structured with respect to elevation while Meynard et al. (2011) found that the correlation to environment was stronger for phylogenetic turnover than for species turnover. Findings such as these suggest the important role of niche conservatism in structuring spatial patterns of phylogenetic turnover.

Importantly for GDM, phylogenetic β diversity indices such as $Sør_{phylo}$ can show a range of dissimilarity between sites, even where no species are shared. Because the biota of those sites are related to differing degrees, dissimilarity also varies, whereas $Sør_{species}$ is saturated (i.e. dissimilarity = 1) where no species are shared. As illustrated in Fig. 1, $Sør_{phylo}$ thus provides for a far broader range of compositional dissimilarity to be included in GDM models. As composition changes along an environmental gradient, if species are replaced by close relatives (more than chance would predict) this progression is reflected in phylogenetic turnover.

Ferrier et al. (2007) proposed that the measure of phylogenetic turnover in Eq. 3 could be used as the biological response variable in a GDM to model phylogenetic turnover, and hence to incorporate phylogenetic relationships into a range of broad scale problems such as environmental classification, conservation assessment, climate-change

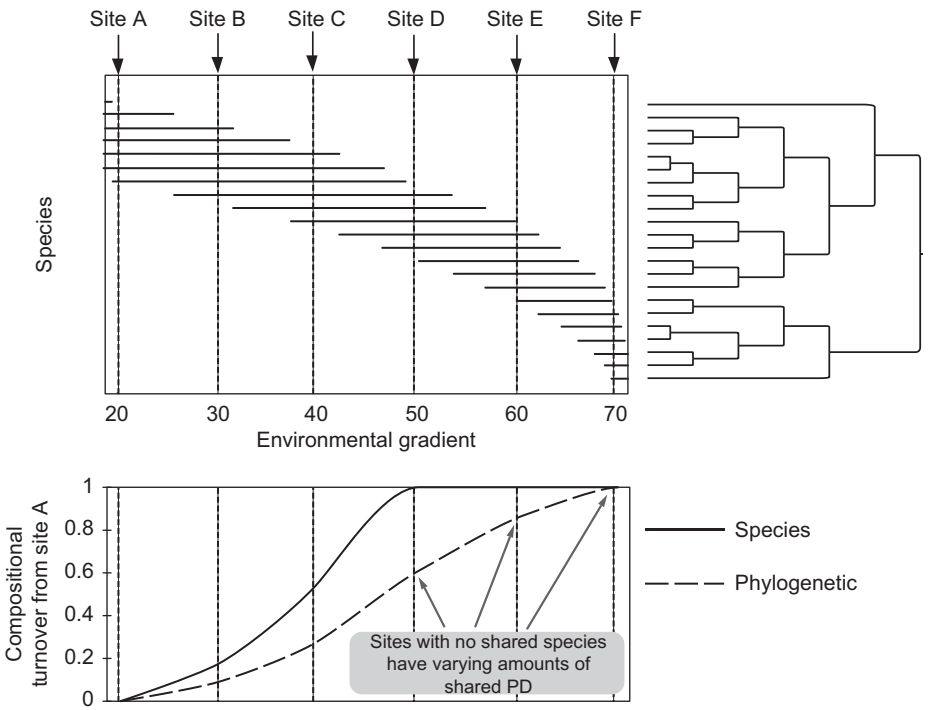


Figure 1. Comparing species and phylogenetic turnover from site A along an environmental gradient. In the lower pane the solid line represents species turnover, comparing each site to site A. This measure is saturated at 1 once no species are shared, so sites D–F have an identical level of dissimilarity from site A despite the species turnover between sites D, E and F. The dashed line, for phylogenetic turnover, reflects the branch lengths shared with site A, measuring compositional dissimilarity including in the absence of shared species, to represent dissimilarity over a larger biological and environmental range. As with all phylogeny based measures, the form of the curve depends on the shape of the phylogeny. Where tree shape approaches a polytomous star, the phylogenetic turnover values approach the species turnover values. Upper pane adapted from Ferrier et al. (2007).

vulnerability assessment and survey gap analysis. This approach was discussed by subsequent authors (Graham and Fine 2008, Faith et al. 2009) but not yet implemented.

## Ancient lineages and current day environment

While the tips on a phylogeny represent currently occurring biota whose distributions are mediated by the present environment, the deeper branches infer past lineages which may have lived in entirely different locations and/or environments to those of their extant descendants. Deep branches on the tree may thus confound rather than strengthen the relationship between phylogenetic and environmental dissimilarity. A determining factor will be the degree to which those phenotypic traits that limit populations to specific environments are conserved within lineages.

If niche conservatism is strong (Donoghue 2008, Crisp et al. 2009, Wiens et al. 2010), and each clade has radiated within a distinct environmental range so that clades represent distinct environments (Graham and Fine 2008), then deep branches should increase the fit of the environment model beyond that for species turnover. In the converse situation where extant members of each clade occur in various environments and their environmental niche is not significantly differentiated from that of other clades, the inclusion of deeper branches would be a confounding factor, reducing model fit.

To implement phylo-GDM we must address these opposing factors in the relationship between phylogenetic turnover and environment. On the one hand we propose that models of compositional turnover in environmental space can be improved by incorporating the similarity in environmental niche between related taxa, but we also know that the correlation of deep branches with current environment may be highly variable. We therefore hypothesise that, compared to a species GDM model, the fit to present-day environments would be strengthened by incorporating phylogenetic relationships between more recently diverged taxa but that deeper branches will cause the model fit to decline as the environmental space occupied by their extant descendants is less differentiated from those of other deep branches.

## Purpose of this paper

Here we present a first implementation of the phylo-GDM approach. We test the relationship between phylogenetic tree depth and GDM model fit for two diverse frog radiations to find the depth at which the relationship between phylogenetic turnover and current environment is strongest. We use the best fitting model for one of these groups, 114 Australian species of the frog family Myobatrachidae, to map the spatial structure of phylogenetic relatedness in the family. We additionally incorporate explanatory

variables for biogeographic isolation to account for divergent evolutionary histories.

## Methods

### Biological data

The Myobatrachidae are frogs found throughout Australia, with several species occurring in New Guinea. A phylogenetic tree was prepared by Scott Keogh, Dale Roberts, Phil Byrne and David Moore (unpublished data 2009), inferred from a maximum likelihood analysis of an alignment of 2467 base pairs of mitochondrial DNA (ND2 and 12s) from 117 species in the family Myobatrachidae as well as one outgroup taxon. Multiple specimens of each species were used to confirm the monophyly of the species, with a single specimen of each species used in the final tree. Three species not occurring in Australia were excluded, as well as ten species of the genus *Uperoleia* which were omitted due to current taxonomic uncertainty (Catullo et al. 2011). The remaining 114 species included in this study represent over 90% of the extant species described for Australia.

The penalised likelihood method was applied to the phylogeny using the program r8s (Sanderson 2003, 2006) to generate a rate smoothed ultrametric tree. The tree resembles a chronogram, with branch lengths broadly proportional to time, but in the absence of dated calibration points, the root of each tree was set to an arbitrary, unitless age of 1, with branch lengths approximating proportions of the total age.

Geolocated species occurrence records were compiled from Australian museum specimens, government surveys and published studies. Taxonomy and locations were checked with relevant authorities (IUCN 2006, Australian Biological Resources Study 2008) and experts on the relevant taxa and region to resolve taxonomic inconsistencies and remove doubtful records. Records known to have a radius of spatial precision $>5000$ m were excluded as were records for taxa not on the phylogeny. The resulting dataset contained 150 669 geolocated records, each linked to the corresponding tree terminal.

These location records were summarized to 0.01° (approximately 1 km) grid cells. Cells with two or more species, or multiple independent collection events, were defined as sites for this analysis. In total, 20 567 sites, representing 59% of sampled cells were available, and were randomly assigned to training and test datasets in the ratio 95% training, 5% test.

A second frog lineage, the Hylidae:Pelodryadinae was included for comparison in the model fit by depth analysis. A phylogeny for 79 of 83 species in this group, based on 1587 bp of 12S and 16S mitochondrial gene sequences (detail in Rosauer et al. 2009) was made ultrametric using the penalised likelihood method described above. The species location data (106 302 records for 76 species in Australia) were prepared as described above to yield 14 214 sites for use in the models.

### Environmental predictors

A total of 64 candidate environmental predictor grids covering terrestrial Australia at the same 0.01° grid resolution used for the species data, were prepared to represent potential drivers of habitat suitability and thus biological composition. They included extremes, means and temporal patterns of solar radiation, temperature, precipitation and water availability, as well as plant productivity, topography, distance to fresh water, soil chemistry and characteristics of the dominant vegetation. These predictors were derived by Williams et al. (2010, 2012 and <spatial.ala.org.au/layers>) following a comprehensive review of available data and its relevance to ecology. We used the procedure described below to select the subset of these predictors most relevant to frog compositional turnover. See Supplementary material Appendix 1, Table A2 for an analysis of their correlation structure.

### Creating the phylogenetic GDM

Generating the phylogenetic GDM model (phylo-GDM) involved three stages. Firstly, we calculated Sørenson dissimilarity between pairs of sites as the response variable in GDM. Secondly, we fitted the GDM model, as described in Ferrier et al. (2007). Thirdly, we used a stepwise variable selection method to simplify the model by removing predictors that made negligible contribution to the overall model fit. These steps are now described in more detail.

We first calculated $Sør_{phylo}$ and $Sør_{species}$ between site pairs drawn from the available sites to create a sites-by-sites dissimilarity matrix for each measure. It is neither computationally practical nor necessary, however, to fill the matrix by sampling all possible pairs of sites. For $n$ sites, the number of possible site-pairs is $\frac{n \times (n-1)}{2}$, so a 20 000 site matrix has $2 \times 10^8$ site pairs. In preliminary tests we found no decline in model performance using a random sample of as few as 75 000 site pairs. We took a conservative approach, however, and used a larger sample of 300 000 site pairs. A complete set of site pairs may not be the most effective sample if the sites are biased in geographic or environmental space with respect to the overall distribution of the taxa of interest as ours were. We used all sites, but balanced site pairs across the study area using a stratified-random sampling method based on site pairs within and between 85 bioregions for Australia (Thackway and Cresswell 1995, DEWHA 2004). We generated the site pairs and measured compositional dissimilarity using the spatial analysis program Biodiverse (Laffan et al. 2010; <www.purl.org/biodiverse>) and Site-Pair Sampler, an add-on module available from the same site.

Phylo-GDM models were fitted with the site pairs described above as the biological response. Software for this step (Manion 2012) is available from <purl.org/gdm>). We used a stepwise process, as outlined by Williams et al. (2012), to select the best set of environment predictors for each model. Groups of similar predictors were tested to find those which contributed to the model. Then with all contributing predictors included, a backwards elimination procedure successively removed predictors contributing $< 0.1\%$ to the deviance explained. By this process, the set of model predictors was simplified from $>35$ to as few as 9 with little decrease in model performance.

## Testing model fit by tree depth

We hypothesised in the introduction that use of phylogenetic information would contribute to a better fitting model, but that the deeper branches on the phylogeny might confound the relationship with current environment. We tested this hypothesis by creating multiple versions of the phylogeny. In each case we removed any branches, or part branches, older than a specified cutoff age, and created a root polytomy at that point. All portions of the tree closer to the tips than this cutoff were retained unchanged (Fig. 2). The effect of this procedure is to disregard older relationships between lineages, treating all lineages which were distinct at the cutoff age as equally distinct. It is analogous to performing an analysis at progressively deeper taxonomic levels, first analysing turnover at species level, then at genus level, then family and so on. A related procedure was briefly described by Ives and Helmus (2010) who collapsed branches at the tips of a tree to isolate the effect of internal branches in the relationship between phylogenetic turnover and environment.

We thus tested the fit of the phylo-GDM model to current environment for the more recent parts of the tree, iteratively testing trees cut at greater depths, to determine the depth of tree which would give the best fit to current environment. A series of 11 trees were created by cutting the tree at progressively deeper points, defined as a proportion of the total age of the tree (Fig. 2), ranging from 0 (include only the terminal taxa, equivalent to the species GDM) to 1 (include the full tree). For each of the 11 trees, $Sør_{phylo}$ was calculated as described earlier.

For consistency in comparing models, we used a common set of predictors that were found to be significant across three tree depths: a full tree (depth = 1), a tree cut at half its depth (depth = 0.5), and tree tips (depth = 0). We fitted a GDM model for each of the eleven tree depths from 0 to 1 and evaluated the relationship between model fit (deviance explained) and tree depth. To gain an initial indication of the generality of this relationship, we repeated this process for the other major frog radiation in Australia, the Hylidae:Pelodryadinae.

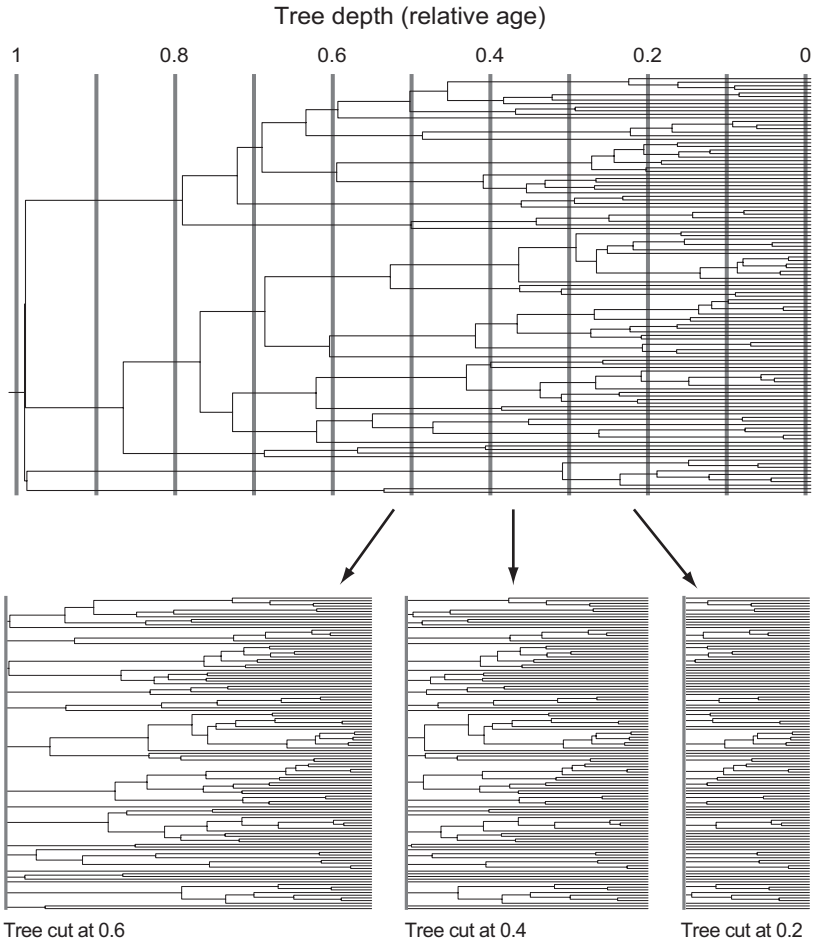


Figure 2. Cutting the phylogenetic tree at different depths. The vertical grey lines indicate potential tree cutting points. In each case, all of the branches right of the line to the tips of the tree, would be included, while anything to the left of the line would be excluded. Three trees, cut at depths of 0.6, 0.4 and 0.2 are illustrated. This procedure generates models which consider only the more recent relationships between lineages. Note that the Sørensen index is unitless, so the fact that the trimmed trees have shorter total branch lengths does not affect the result. What does affect the result is that the shared evolutionary history between taxa is only counted if it occurred closer to the tips than the cut point, so the shared component of branch length reduces as the tree is truncated. Once the tree is cut closer to the tips than the most recent node, the dissimilarity measure is equivalent to species dissimilarity, as there are no shared branches.

### Biogeographic adjustment

We introduce a procedure for incorporating explanatory variables aimed at addressing the effects of broad-scale biogeographic isolation on the divergence of evolutionary histories, thereby helping to account for patterns of compositional dissimilarity which are unrelated to measures of current-day environment. Where environmentally similar areas have different biota, for example due to current or past dispersal barriers, a model based solely on environmental attributes would underestimate the compositional dissimilarity between such areas. For example, the south-east of the State of South Australia and south-western Australia, separated by over 2000 km, are relatively similar environmentally but have very different biota, having been separated by sea and then desert for perhaps 15 million yr with deep splits for many frog and plant lineages (Crisp et al. 2004, Morgan et al. 2007).

To incorporate these biogeographic disjunctions into the model, we used the Australian bioregions (DEWHA 2004) as spatial units of analysis. We calculated the mean Pearson residual (based on the difference between observed and predicted Sørensen dissimilarities) for site-pairs between each pair of bioregions. These averaged residuals quantified where the model consistently over or under estimated the actual degree of phylogenetic dissimilarity between sites in the two regions of interest.

To guard against model overfitting, the resulting regions-by-regions residuals matrix was transformed by multi-dimensional scaling (MDS) to generate axes accounting for the general pattern of residuals across all regions. The first 3 MDS axes were used to generate biogeographic predictor grids, reflecting the trends in compositional turnover between regions that were not accounted for by the environmental model. These biogeographic predictor grids were used in the same manner as the initial set of environmental predictor grids. The model was then rerun with both the environmental and biogeographic predictors.

This approach does not explicitly distinguish residuals from the environmental model which are due to vicariance, from those due to other factors (e.g. missing environmental predictors, sampling error or local site history). It is selective however, in accounting only for those factors which represent a general trend in compositional dissimilarity between multiple geographic regions. In this way it captures a component of the spatial structure of turnover at a broad scale which was not included in the environmental model. This use of residuals would be circular if used to test hypotheses about compositional turnover between bioregions. The purpose here however is to better interpolate the observed patterns beyond sampled sites. We compared the strength of model predictions for the independent test dataset of site-pairs derived from the 5% of sites held aside for testing.

### Visualising spatial patterns of phylogenetic turnover

To visualise the spatial structure of phylogenetic turnover, we clustered all grid-cells in the study area into 300 classes based on UPGMA hierarchical classification of predicted $Sør_{phylo}$ (Ferrier et al. 2007) and coloured each class based on multi-dimensional scaling of predicted similarity, such that similar colours indicate compositional similarity (Belbin et al. 1983).

## Results

### Phylogeny extends measurement of compositional turnover

A comparison of the $Sør_{phylo}$ and $Sør_{species}$ results for the same site pairs (Fig. 3) confirms that $Sør_{phylo}$ differentiates turnover between site pairs which are of equal dissimilarity (i.e. 1) for $Sør_{species}$ because they share no species. Whereas the $Sør_{species}$ values are concentrated at 1 for most of the ecological distance spectrum, $Sør_{phylo}$ values below one predominate (Fig. 4a) until nearly the furthest class of ecological distance (Fig. 4c).

As hypothesised, including recent phylogenetic relationships maintained or improved the fit of phylo-GDM models relating compositional turnover and current environment. The 'age' at which the model fit is strongest, and the amount of improvement and subsequent decline, differed between the two families (Fig. 5). There was only a very small increase in fit for Myobatrachidae, but in both families including the full tree (tree depth = 1) gave a substantially weaker model fit than the species turnover model (tree depth = 0).

### Predictors of phylogenetic turnover

Of the candidate environmental predictors tested, 19 were selected for Myobatrachidae (Supplementary material Appendix 1, Fig. A1). The candidate predictors represent relatively independent groupings of environment related to climate, substrate, terrain and vegetation, and as expected based on a conceptual understanding of species–environment relationships, representatives from each of these broad environmental groups were included in the

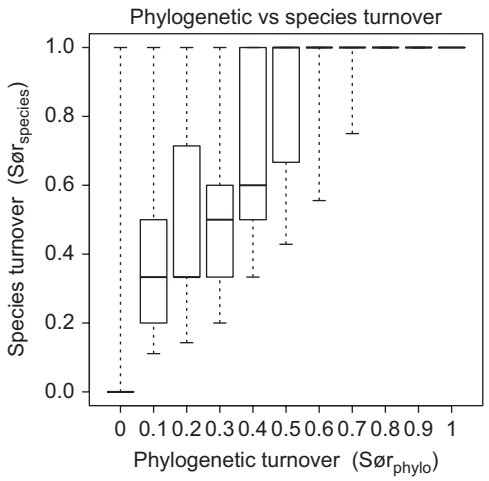


Figure 3. Phylogenetic versus species turnover for family Myobatrachidae. Where the $Sør_{species}$ value is 1, $Sør_{phylo}$ has a broad range of values, giving information about compositional dissimilarity where no species are shared. Each box represents the interquartile range, and dashed lines the full range.

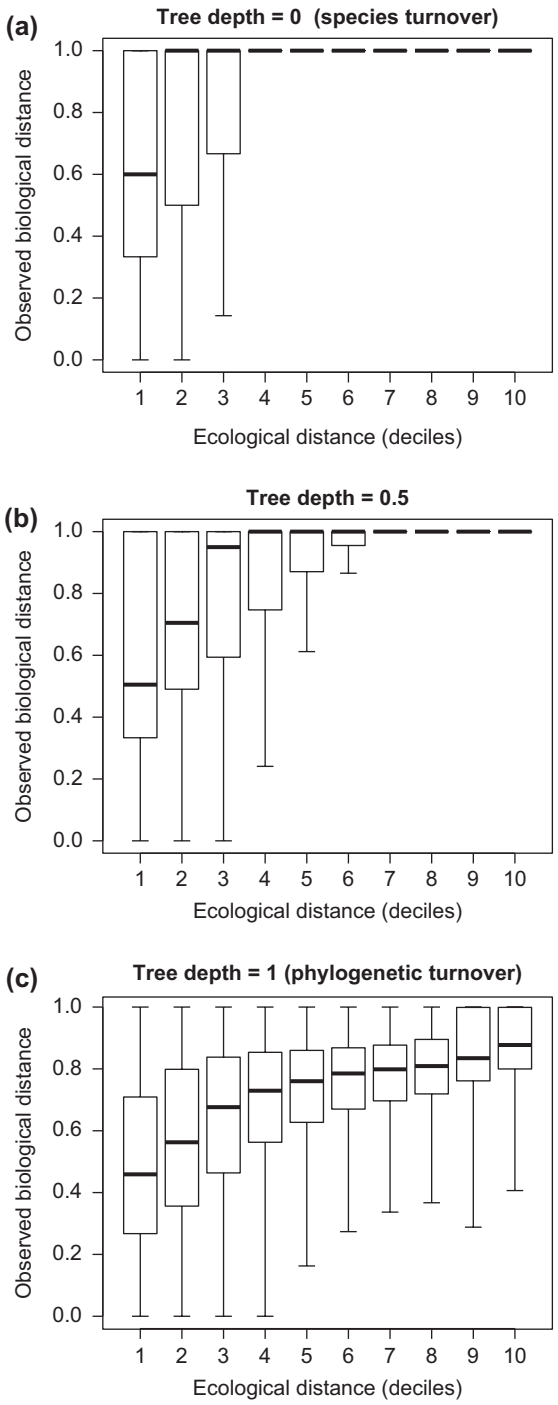


Figure 4. Compositional turnover versus ecological distance for measures of turnover. Phylogenetic information extends discrimination of compositional difference to more ecologically dissimilar sites. (a) $Sør_{species}$ (tree depth 0) is 1 (no shared species) for all site pairs except in the closest 30% of sites by ecological distance. In contrast (c) $Sør_{phylo}$, (tree depth = 1) displays a broad range of values for almost the whole ecological distance range, delivering far more information about the compositional similarity between sites. (b) using only the more recent phylogenetic relationships, displays an intermediate pattern. Vertical boxes represent the interquartile range, dotted lines a further twice the interquartile range.

model (Supplementary material Appendix 1, Table A1). The most important predictor of phylogenetic turnover was the degree of summer or winter rainfall precipitation. This factor captures the gradient from predominantly winter rainfall in southern Australia to summer rainfall in northern Australia. The plant growth indices representing the interaction between radiation, temperature and water availability generated using the GROCLIM module of ANUCLIM (Hutchinson et al. 2000) were also strong predictors, as were indices of slope, minimum monthly solar radiation and the maximum rate of change in precipitation within the annual cycle, the latter being an indicator of seasonal shifts in phenology (Williams et al. 2012). As with any correlative model, specific environmental correlates of turnover in these GDM models may suggest, but do not indicate, causality.

## Spatial pattern of turnover

Figure 6 shows the spatial pattern of compositional similarity predicted by the phylo-GDM model for the Myobatrachidae with tree depth of 0.4. Several distinct areas for myobatrachid diversity are evident including the Wet Tropics (A), the Central East Coast (B), the south-east and Tasmania (C), the south-west of Western Australia (D), and the Pilbara and Arid Zone (E). This reflects the areas of myobatrachid endemism identified by Slatyer et al. (2007) in tropical Queensland and in south western Australia, but not those in the Northern Territory or Kimberley, potentially due to omission of a number of *Uperoleia* species from the study.

## Biogeographic adjustment

With inclusion of the biogeographic predictors, the model distinguished more strongly between environmentally similar but compositionally distinct areas. For example, the south-west of Western Australia is shifted further in phylogenetic dissimilarity from south-eastern Australia than is predicted without this adjustment, due to their relatively similar environments (Fig. 7). The greatest reduction in model residuals was achieved between two environmentally similar, but biogeographically separated areas, the Esperance (A) and Kanmantoo (B) bioregions (Fig. 7) spanning the east-west divide. The biogeographic adjustment increased the mean prediction of dissimilarity between these regions from 0.70 to 0.92, bringing it closer to the observed value. This improvement in predictive performance is typical of results for other regions separated by this east-west divide. We observed a small improvement in the overall model performance, with the correlation of predicted to observed $Sør_{phylo}$ increasing from 0.57 to 0.59. Importantly, this improvement was confirmed for independent test sites, where the correlation increased from 0.52 to 0.55.

## Visualising phylogenetic turnover

GDM class colour maps appear to reflect the full result of a GDM model, but they are in fact just one summary of predicted turnover. Unlike a traditional occurrence model

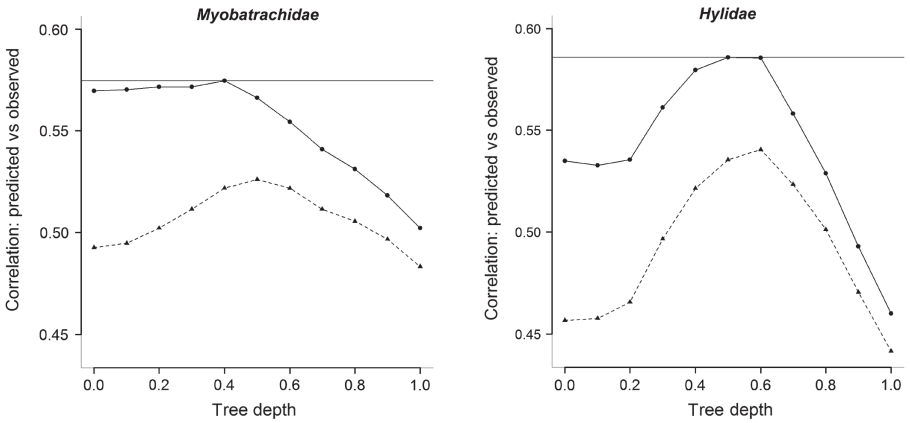


Figure 5. Correlation (r) between observed Sør and the GDM prediction, over a spectrum of tree depths from a species GDM model (depth = 0) to a full phylo-GDM model (depth = 1). Correlations to two expressions of the GDM prediction are shown – dotted line for transformed ecological distance, and solid line for predicted Sør. Both models show improvement in their prediction of compositional turnover with inclusion of the more recent relationships between species, but a sharp decline with inclusion of deeper branches.

where the result for each pixel is a single number (z) such as likelihood of occurrence (Phillips et al. 2006), here the model result for each pixel represents a vector of dissimilarity to all other pixels ($z_1$, $z_2$, $z_3$, … $z_n$), and thus a given map conveys only part of the model result. In Fig. 8 more detail is shown by using the full colour spectrum to represent the pattern of phylogenetic turnover at a regional scale as predicted by the continental model. The area shown, comprising four bioregions in eastern Australia, is the most speciose area for Myobatrachidae (Slatyer et al. 2007). The coastal plain (green), cooler, heavily dissected escarpment (purple) and the drier country further inland (pink) each show their own pattern in phylogenetic turnover, consistent with turnover above species level from a coastal assemblage to montane specialists such as *Philoria* and then arid adapted genera such as *Neobatrachus*.


Figure 6. Classification by predicted phylogenetic similarity for myobatrachid frogs. Similar colours predict phylogenetically similar areas (low $Sør_{phylo}$) based on the phylogeny limited to depth 0.4. The colours are generated by performing a multi-dimensional scaling on a matrix of predicted dissimilarities. The first 3 ordination axes are used to define in 3 dimensions (red, green, blue) the colour allocated to each area. The model result is presented as similarity or difference of colour between areas, but the specific colours do not translate to a linear progression of values.

## Discussion

The phylo-GDM technique presented here is a novel approach to analysing and predicting the structure of spatial turnover in assemblage phylogenetic composition. GDM has proved informative for unravelling the relationships between isolation and environment as drivers of genetic and morphological differentiation within species (Thomassen et al. 2010, 2011, Smith et al. 2011), and here we have shown how it can also be used to model ancestral relationships between species. In particular, because the incorporation of phylogeny delivers information about compositional turnover at larger ecological distances where there may be no or few shared species, we found that phylogenetic dissimilarity can provide a more informative indication of the broad-scale spatial structure of biodiversity than a measure based purely on species composition. For similar reasons this approach can provide more information on relationships between less speciose sites. For example, $Sør_{species}$ between two single-species sites is polarised, with only two possible results, 0 (the same species) or 1 (different species), but the $Sør_{phylo}$ measure reflects the degree of phylogenetic relatedness, and provides more information about the compositional differences.

Including phylogenetic relationships between recently diverged lineages in the biological response data for a GDM provided a better link between turnover and environment, although the magnitude of the improvement varied between families. By selecting the appropriate scope of phylogenetic information (tree depth), the model performed better than a species GDM model. Depth selection is important, because in our tests, a model based on the full tree performed substantially less well than either the optimal tree depth or a species GDM.

The improvement in model fit which we observed could be expected so long as more closely related lineages tend to occur in similar environments. This can come about for a

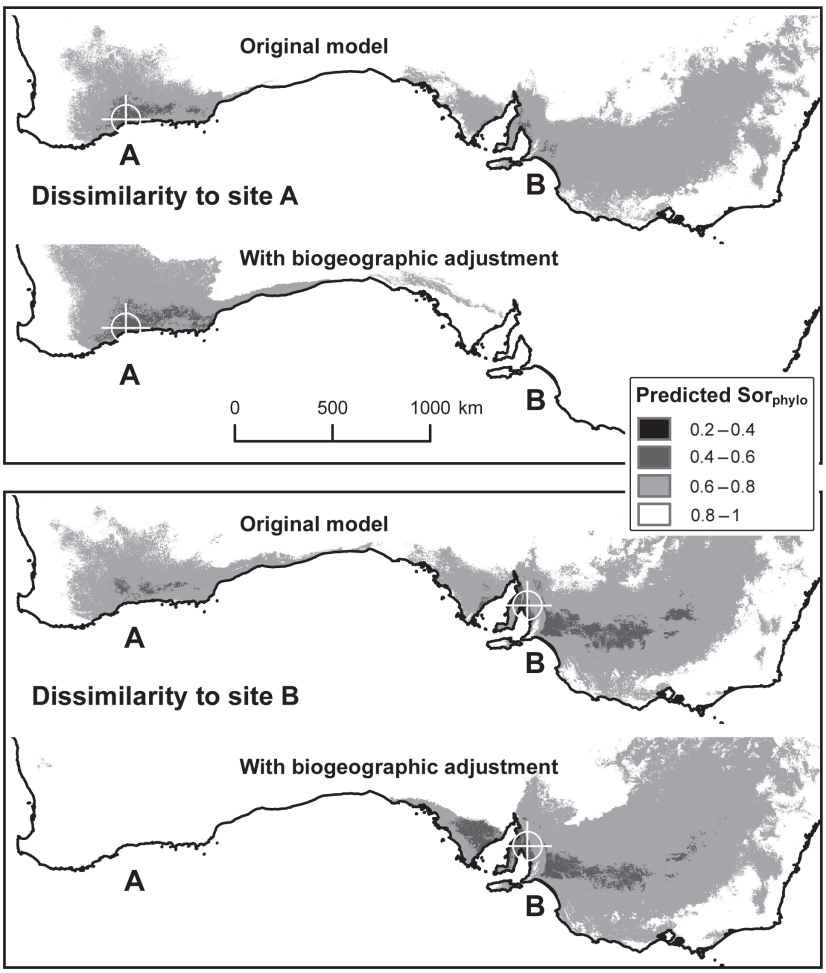


Figure 7. Predicted phylogenetic dissimilarity from marked site (white cross hairs) for Myobatrachidae with and without biogeographic adjustment. $Sør_{phylo}$ is based on the phylogeny to depth 0.4. With biogeographic adjustment, the average dissimilarity predicted between sites in regions at A and B increases from 0.70 to 0.93 which is close to the observed value. The over-prediction of similarity across barriers such as the Nullarbor desert, is thus avoided.

combination of two reasons: firstly, the more closely related species have retained adaptations which suit them to similar environments (niche conservatism), and secondly, recent common ancestry in a given area often means that closely related lineages are more likely to occur near to each other (if not at the same sites) and hence share more similar environments (Freckleton and Jetz 2009). Neither of these processes is captured by a species GDM model. It would be useful to test the effects of these two processes on phylo-GDM in a simulation where the degree of ancestral influence on the current geographical and environmental range of species can be explicitly defined (Colwell and Rangel 2010).

The increase in model fit to mid tree depths for Hylidae (Fig. 5) shows that the clades with an origin between 0.2 and 0.6 of the crown age of the group are, on average, well structured in environmental space. This pattern is consistent with other studies (Bryant et al. 2008) and would happen if these mid-age lineages occupied distinct environmental zones which have been conserved across current species, in addition to the structure of species composition in environmental space. The Myobatrachidae showed a slightly stronger relationship between species turnover and environment than the hylids, but the minimal improvement with inclusion of phylogenetic data indicates a far weaker distinction between the environmental spaces occupied by different clades.

A tree depth analysis of the type performed here could also be relevant to studies of niche evolution through changing environments. Further research could consider the form of the relationship from both a theoretical and empirical perspective, relating known paleo-climatic events to the dates implied by a temporal analysis of model fit, and comparison to established methods which test niche evolution in a spatial context (Freckleton and Jetz 2009, Cooper et al. 2011). Our principal aim in this study however was simply to provide the best GDM model fit, and to assess the extent to which current patterns of phylogenetic turnover could be modelled, with a focus on improved surrogate information for biodiversity assessment and conservation planning (Ferrier 2002).

An appropriately fitted and tested phylo-GDM model can make phylogeographic information available for a broad range of applications. The results of such an analysis could be applied to questions of biological survey design, reserve planning (Allnutt et al. 2008) and climate-change adaptation (Fitzpatrick et al. 2011). Where phylo-GDM outperforms species models, the method may actually be useful where a

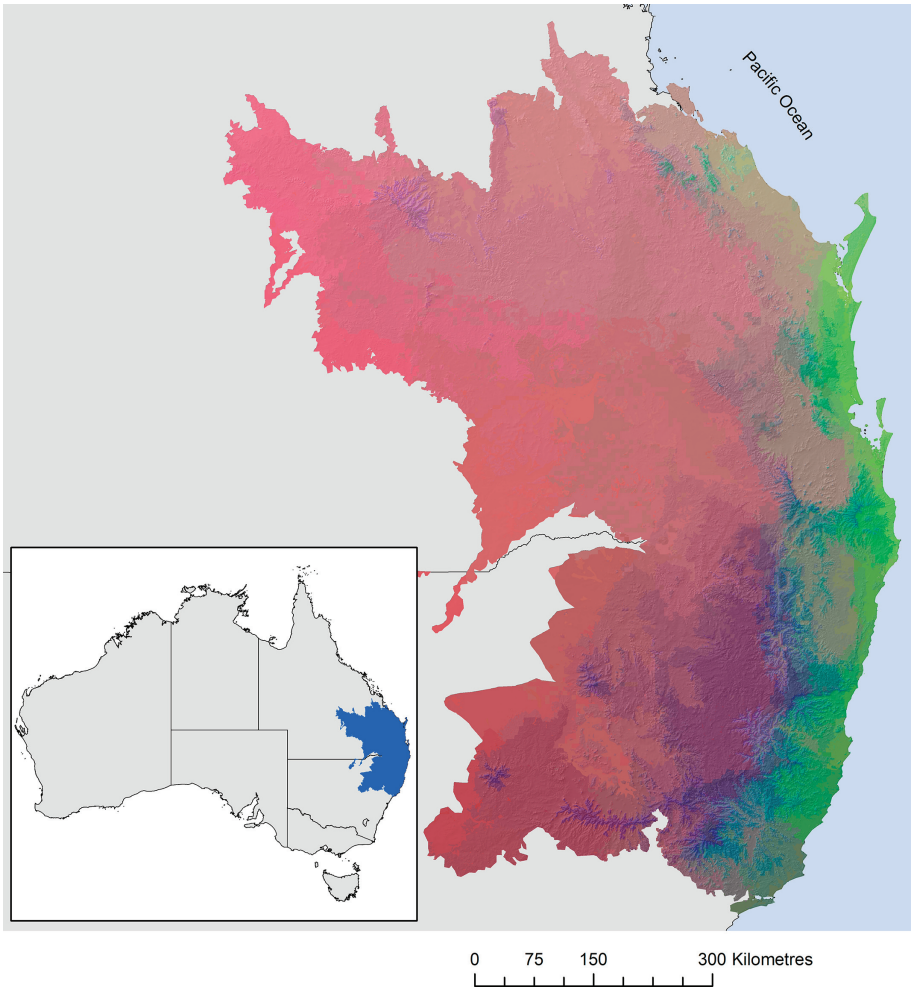


Figure 8. GDM classification for family Myobatrachidae by phylogeny to depth 0.4 for an area of central eastern Australia. The area comprises the Brigalow Belt South, Nandewar, New South Wales North Coast and South East Queensland bioregions. As for Fig. 6, similar colours represent a prediction of phylogenetic similarity (low $Sør_{phylo}$).

strong representation of the spatial pattern of biodiversity is required, even if the question is not about the phylogenetic relationships per se.

Phylo-GDM may also be relevant to studies in phylogeography and macroecology dealing with the evolution and maintenance of diversity at various spatial and taxonomic scales. It removes the need to work at species level, and to use named taxa, where phylogenetic data are available. Phylogenetic turnover can be calculated for any operational taxonomic units (OTUs) whose locations and phylogenetic relationships are known, so the same technique could be used to model spatial structure in biodiversity composition in situations where taxonomic identification is not possible or not practical. By including lineages directly via their molecular signature, phylo-GDM could thus broaden the range of taxa and data sources that can be included in conservation assessments, to incorporate biological groups that are currently not considered due to a lack of reliable taxonomic determinations at the species level or where OTUs have been generated from environmental metagenomic (ecogenomic) sequencing (Chariton et al. 2010, Steele and Pires 2011). In cases where there is a significant amount of gene flow between lineages however, a model based on genetic distance (Thomassen et al. 2010) may be more appropriate.

Importantly, phylo-GDM provides testable predictions. For example, the model may indicate areas of phylogenetic endemism (Rosauer et al. 2009) – i.e. locations predicted to be highly dissimilar from all other areas. Where this prediction differs from current knowledge, the null hypothesis must be that the model is not predicting well for that area. Testing and potentially rejecting this null hypothesis however could involve using the model predictions to target new surveys or genetic sampling to identify distinct lineages predicted by the model.

The GDM technique models the spatial structure of compositional turnover but does not incorporate alpha diversity. This means that highly diverse areas (high species richness or PD) are not distinguished in the model from less diverse areas where the proportion of turnover is equivalent. It may be possible to address this for phylo-GDM by extending the technique for integrated modelling of $\alpha$ and $\beta$ diversity developed by Mokany et al. (2011).

Our method for incorporating biogeographic history aims to address an important challenge for GDM and other environmental modelling techniques (including single

species distribution models). That is, where compositional similarity is erroneously inferred between areas with similar environments. By including separate regional contributions to turnover in addition to the environmental contribution, the overall fit between predicted and observed dissimilarity is improved, both within the model, and for independent test sites not used in model fitting.

The biogeographic adjustment method results in a more accurate model of turnover, but at a cost to local scale accuracy across region boundaries. Further investigation would ideally lead to a method which captures the spatial structure of this additional component of turnover, without introducing any a priori boundaries into the model. One option may be to use a cost-distance analysis based on suitability of the intervening habitat, to represent evolutionary isolation (Graham et al. 2006). Such an approach would ideally account for the duration of isolation. Alternatively, one could introduce a priori boundaries based on known biogeographic disjuncts, and test their explanatory power in a model selection framework.

### Conclusions

The phylo-GDM method presented here is potentially a significant step forward in the spatial modelling of biological diversity. By using a more discriminating measure of diversity, this technique can establish an equal or stronger relationship between compositional patterns and current environment. It provides new opportunities to include more recent evolutionary relationships in spatial analyses, and may create a useful avenue to apply the growing volume of sequence-only biological field data into conservation assessment. Perhaps of greatest interest, it provides testable, spatially continuous predictions of phylogeographic patterns.

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Supplementary material (Appendix ECOG-00466 at <www.oikosoffice.lu.se/appendix>). Appendix 1.

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