Phylogenetic Inference using RevBayes

Historical biogeography

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1 Introduction

How did species come to live where they're found today? Observing where species live today, we can leverage phylogenetic and geological information to model their distribution as the outcome of biogeographic processes to answer this. These natural processes require some additional considerations, such as how ranges are inherited following speciation events, and how geological events might influence dispersal rates. Using Revbayes for biogeographic inference, standard Bayesian techniques are available, such as model selection, Metropolis-coupled MCMC, and stochastic mapping. This tutorial describes how to perform Bayesian inference of historical biogeography using RevBayes. Currently, this primarily covers range evolution models, where a species may occupy multiple discrete areas simultaneously. Tutorials to model individual specimens' geographical locations (sometimes called phylogeographic models) are under development.

Outline

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2 Dispersal-Extinction-Cladogenesis model

2.1 Model and method

First, we define the range for taxon i as the bit vector X_i, where $X_{i,j} = 1$ if the taxon is present in area j and $X_{i,j} = 0$ if the taxon is absent. Each taxon range is a bit vector of length N areas. For example, if taxon B is present only in areas 2 and 3 out of $N = 3$ areas, its range is represented as $X_B = (0, 1, 1)$, which is translated to the bit string $X_B = 011$ for short. If we apply the labels A, B, and C to our three areas, this bit vector can also be represented as a set: $X_B = 011$ is the same as $X_B = \{B, C\}$, or $X_B = BC$ for short. The data matrix, $\mathbf{X}$, is analogous to a multiple sequence alignment where each element in the data matrix reports a discrete value for a homologous character shared by all taxa at column j.

2.2 Modeling anagenic range evolution

Next, we need a model of anagenic range evolution. Since we have discrete characters we'll use the continuous-time Markov chain, which allows us to compute transition probability of a character changing from i to j in time t through matrix exponentiation

$$\mathbf{P}_{i,j}(t) = \left[\exp\left\{\mathbf{Q}t\right\}\right]_{i,j},$$

where $\mathbf{Q}$ is the instantaneous rate matrix defining the rates of change between all pairs of characters, and $\mathbf{P}$ is the transition probability rate matrix. This technique of matrix exponentiation is powerful because it integrates over all possible scenarios of character transitions that could occur during t so long as the chain begins in state i and ends in state j. Remember, i and j represent different ranges, each of which is encoded as a set of occupied areas.

We can then encode range evolution events into the allowed character transitions of $\mathbf{Q}$ and parameterize the events so that we may infer their relative importance to generating our observed ranges. We'll take a simple model of range expansion (e.g. $BC \rightarrow ABC$) and range contraction (e.g. $BC \rightarrow C$). (Range expansion may also be referred to as dispersal or area gain and range contraction as extirpation or area loss.) The rates in the transition matrix for three areas might appear as

$$\mathbf{Q} = \begin{array}{c|cccccccc} & \emptyset & A & B & C & AB & AC & BC & ABC \\ \hline \emptyset & - & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ A & e_A & - & 0 & 0 & d_{AB} & d_{AC} & 0 & 0 \\ B & e_B & 0 & - & 0 & d_{BA} & 0 & d_{BC} & 0 \\ C & e_C & 0 & 0 & - & 0 & d_{CA} & d_{CB} & 0 \\ AB & 0 & e_B & e_A & 0 & - & 0 & 0 & d_{AC} + d_{BC} \\ AC & 0 & e_C & 0 & e_A & 0 & - & 0 & d_{AB} + d_{CB} \\ BC & 0 & 0 & e_C & e_B & 0 & 0 & - & d_{BA} + d_{CA} \\ ABC & 0 & 0 & 0 & 0 & e_C & e_B & e_A & - \end{array},$$

where $e = (e_A, e_B, e_C)$ are the (local) extinction rates per area, and $d = (d_{AB}, d_{AC}, d_{BC}, d_{CB}, d_{CA}, d_{BA})$ are the dispersal rates between areas.

Q: For the three-area DEC rate matrix above, what is the rate of leaving state 101? That is, what is the absolute value of the diagonal term in the rate matrix for $Q_{AB,AB}$?

Note the rate of more than one event occurring simultaneously is zero, so a range must expand twice by one area in order to expand by two areas.

Q: What events might explain a transition from range ABC to range A? From range AB to range C?

Of course, this model can be specified for more than three areas.

Q: Imagine a DEC rate matrix with four areas, $ABCD$. What would be the dispersal rate for $Q_{BC,BCD}$? How many states does a DEC rate matrix with four areas have? What is the relationship between the number of areas and the number of states under the DEC model?

Let's consider what happens to the size of $\mathbf{Q}$ when the number of areas, N, becomes large. For three areas, $\mathbf{Q}$ is size 8×8. For ten areas, $\mathbf{Q}$ is size $2^{10} \times 2^{10} = 1024 \times 1024$, which approaches the largest size matrices

that can be exponentiated in a practical amount of time. For biogeographic inference under large numbers of areas, see the Tutorial XXX (**?**).

2.3 Modeling cladogenic range evolution

In addition to dispersal and extinction, the DEC models cladogenic range evolution events. For each internal node in the reconstructed tree, one of two cladogenic events can occur: sympatry or allopatry. Say the range of a species approaching an internal node, i.e. that is about to speciate, is A. Since the species range is size one, this always results in sympatry, where both daughter lineages inherit the ancestral species range, so both lineages begin in state A. The notation $A \rightarrow A \mid A$ describes this event: the state is A before cladogenesis, the left daughter inherits range A after cladogenesis, as does the right daughter.

Now suppose the ancestral range is ABC. Under sympatric cladogenesis, one lineage identically inherits the ancestral species range, ABC, while the other lineage inherits only a single area, i.e. only A or B or C.

Under allopatric cladogenesis, the ancestral range is split evenly among daughter lineages, e.g. one lineage may inherit AB and the other inherits C. Both daughter lineages inherit the entire ancestral species range following widespread sympatric cladogenic events. For a general description of state transitions for cladogenic events, see **?**.

Q: What are the 6 possible states in the daughter lineages after cladogenesis given the state is AB before cladogenesis?

The probabilities of anagenic change along lineages must account for all combinations of starting states and ending states. For 3 areas, there are 8 states, and thus $8 \times 8 = 64$ probability terms for pairs of states. For cladogenic change, we need transition probabilities for all combinations of states before cladogenesis, after cladogenesis for the left lineage, and after cladogenesis for the right lineage. Like above, for three areas, there are 8 states, and $8 \times 8 \times 8 = 512$ cladogenic probability terms.

Q: For three areas, there are $3 + 12 + 6 = 21$ possible sympatry events and $6 + 6 = 12$ possible allopatry events. How many terms in the cladogenesis matrix are zero?

The DEC model ignores speciation events hidden by extinction or incomplete taxon sampling. The probability of cladogenesis and local extinction events would ideally be linked to a birth-death process, as it is in the GeoSSE model (**?**). Unfortunately, since the numerical method for SSE models scale poorly, and DEC models remain the only option when the geography has more than two or three areas. For more than ten areas, we need data augmentation to integrate over range evolution, which is used in Section XXX.

The rest of this section will describe how to run a simple DEC analysis using RevBayes.

2.3.1 Specifying a simple DEC model

We'll use a dataset for 23 primates, which are the same taxa as used in Section XXX. To keep the model simple, we'll ranges are over three areas: the New World, Africa, and Eurasia. For simplicity, we'll assume their phylogeny is time-calibrated, errorless, and fixed.

First, set your working directory,

```
setwd("/Users/arwallace/projects/RB_Biogeography_tutorial/")
```

create some `String` variables for file handling,

```
fp = "./"
data_fn = fp + "data/primates_bg_n3.tsv"
tree_fn = fp + "data/primates.tree"
out_fn = fp + "output/bg_1"
```

then read in our character data,

```
data = readTSVCharacterData(data_fn, type="NaturalNumbers")
```

and our tree

```
tree <- readTrees(tree_fn)[1]
```

Next, compute the number of states from the number of areas

```
n_areas = data.nchar()
n_states = 2^data.nchar()
```

Declare index variables for our move and monitor vectors for future use

```
mvi = 1
mni = 1
```

Now, we'll begin to construct the rate matrix for anagenic events. First create a matrix, 8-by-8 in size, initialized with all zeroes

```
for (i in 1:n_states) {
    for (j in 1:n_states) {
        r[i][j] <- 0.
    }
}
```

Now we need to populate the non-zero rate matrix elements, which are in terms of dispersal and extinction rates. We'll use one dispersal rate and one extinction rate for this tutorial, and explore more complex models in later sections.

First, create a extinction rate parameter and assign it a scale move

```
r_e ~ dnExp(10.)
mv[mvi++] = mvScale(r_e, weight=5)
```

Before assigning the rates to the rate matrix, we'll create a vector to hold the per-area extinction rates

```
for (i in 1:n_areas) {
    e[i] := r_e
}
```

Now create the dispersal rate and scale move

```
r_d ~ dnExp(10.)
mv[mvi++] = mvScale(r_d, weight=5)
```

then assign the between-area dispersal rates as determined by r_d

```
for (i in 1:n_areas) {
    for (j in 1:n_areas) {
        if (i != j) {
            d[i][j] := r_d
        }
    }
}
```

Next, we'll populate the non-zero rate matrix elements. Rates are indexed by the natural number value of the range, e.g. the range spanning Eurasia and Africa is coded as 011, which is state 4.

First assign the extinction (range loss) rates

```
r[4][2] := e[2]              # 011 -> 001 : Extirpate in area 2
r[4][3] := e[3]              # 011 -> 010 : Extirpate in area 3
r[6][2] := e[1]              # 101 -> 001 : Extirpate in area 1
r[6][5] := e[3]              # 101 -> 100 : Extirpate in area 3
r[7][3] := e[1]              # 110 -> 010 : Extirpate in area 1
r[7][5] := e[2]              # 110 -> 100 : Extirpate in area 2
r[8][4] := e[1]              # 111 -> 011 : Extirpate in area 1
r[8][6] := e[2]              # 111 -> 101 : Extirpate in area 2
r[8][7] := e[3]              # 111 -> 110 : Extirpate in area 3
```

then the dispersal (range gain) rates

```
r[2][4] := d[3][2]           # 001 -> 011 : Disperse from area 3 to 2
r[2][6] := d[3][1]           # 001 -> 101 : Disperse from area 3 to 1
r[3][4] := d[2][3]           # 010 -> 011 : Disperse from area 2 to 3
r[3][7] := d[2][1]           # 010 -> 110 : Disperse from area 2 to 1
r[5][6] := d[1][3]           # 100 -> 101 : Disperse from area 1 to 3
r[5][7] := d[1][2]           # 100 -> 110 : Disperse from area 1 to 2
r[4][8] := d[2][1] + d[3][1] # 011 -> 111 : Disperse from area 2 to 1 and from 3 to 1
r[6][8] := d[1][2] + d[3][2] # 101 -> 111 : Disperse from area 1 to 2 and from 3 to 2
r[7][8] := d[1][3] + d[2][3] # 110 -> 111 : Disperse from area 1 to 3 and from 2 to 3
```

Show the value of `r` and compare it to the matrix in Equation (XX).

Of course we did not need to declare `d` and `e` to assign `r`, but we'll see these intermediate variables act as a template expose the structure of `r` for modification.

So far, we only have the desired parameterization of the rate matrix, but we still haven't created a rate matrix function. Converting the vector-of-vectors, `r`, into a simplex allows us to use existing rate matrix functions.

First, we'll convert `r` into a one-dimensional vector, skipping the diagonal elements.

```
k <- 1
for (i in 1:n_states) {
    for (j in 1:n_states) {
        if (i != j) {
            er_nat[k] := r[i][j]
            k += 1
        }
    }
}
```

Finally, normalize `er_nat` using a simplex, then pass the resulting exchangeability rates as arguments into the rate matrix function, `q`.

```
er := simplex(er_nat)
bf <- simplex(rep(1,n_states))
q := fnFreeK(er, bf)
```

This yields the desired three-area DEC rate matrix modeling anagenic character change. In contrast, cladogenic event probabilites are given by a transition probability matrix and do not require a rate matrix.

First, we will create a vector of prior weights on cladogenesis events. Here, we assign a flat prior to all cladogenic events

```
widespread_sympatry_wt <- 1.0
subset_sympatry_wt   <- 1.0
allopatry_wt         <- 1.0
clado_prior          <- [ widespread_sympatry_wt, subset_sympatry_wt, allopatry_wt ]
```

then create the distribution over cladogenic event types and add its MCMC move

```
clado_type           ~ dnDirichlet(clado_prior)
mv[mvi++]             = mvSimplexElementScale(clado_type, alpha=10, weight=5)
```

To give the simplex elements descriptive names when monitored, assign the values to deterministic nodes

```
widespread_sympatry  := clado_type[1]
subset_sympatry      := clado_type[2]
allopatry            := clado_type[3]
```

Then create the cladogenic transition probability matrix

```
b <- simplex(1,1)
clado_prob := fnCladoProbs(clado_type_prob, b, n_areas, 2)
```

Add a parameter for a biogeographical clock, which scales the overall rate of range evolution. As a prior, an exponential distribution with rate 10 generates one dispersal or extinction event per 10 million years.

```
clock_bg ~ dnExp(10)
mv[mvi++] = mvScale(clock_bg, weight=5)
```

Finally, all our model components are encapsulated in the `dnPhyloCTMCClado` distribution, which is similar to `dnPhyloCTMC` except specialized to integrate over cladogenic events. Although this dataset has three areas, it is recognized single character with states valued from 1 to 2^3, hence `nSites=1`.

```
m ~ dnPhyloCTMCClado( tree=tree, Q=q, cladoProbs=clado_prob, branchRates=clock_bg,
    nSites=1, type="NaturalNumbers" )
```

The remaining tasks should be familiar by now, so we can proceed briskly. Attach the observed ranges to the model.

```
m.clamp(data)
```

Compose the model.

```
mdl = model(m)
```

Add the monitors.

```
mn[mni++] = mnScreen(clock_bg, d[1][2], d[1][3], d[2][1], d[2][3], d[3][1], d[3][2], e
    [1], e[2], e[3], widespread_sympatry, subset_sympatry, allopatry)
mn[mni++] = mnFile(clock_bg, d[1][2], d[1][3], d[2][1], d[2][3], d[3][1], d[3][2], e[1],
     e[2], e[3], widespread_sympatry, subset_sympatry, allopatry, file=out_fn+".params.
    txt")
```

Create the MCMC object, and run the chain after burn-in.

```
ch = mcmc(mv,mn,mdl)
ch.burnin(1000, 10)
ch.run(10000)
```

2.3.2 Per-area rates

Biologically, local extinction events probably do not occur at equal rates across all areas, as done above. Ecological factors, geographical distances, etc. might cause these parameters to be weakly correlated or

completely uncorrelated. Dispersal rates, also, might not be the same between pairs of areas, or even symmetric depending on the direction of dispersal. Rather than constraining all events of a type to share a common rate, instead you might give each area it's own extinction parameter

```
for (i in 1:3) {
    e[i] ~ dnExp(10.)
    mv[mvi++] = mvScale(e, weight=5)
}
```

or give each ordered pair of areas a it's own dispersal rate

```
for (i in 1:3) {
    for (j in 1:3) {
        if (i != j) {
            d[i][j] ~ dnExp(10.)
            mv[mvi++] = mvScale(d[i][j], weight=5)
        }
    }
}
```

This parameterization is identical to matrix introduced in Eq XXX. In Section XXX, we'll extend this idea further to parameterize features of range evolution, and incorporate paleogeological information.

2.3.3 Exercises

- Widespread sympatric speciation is thought to be evolutionarily rare. Set the Dirichlet prior on cladogenic event types to heavily disfavor these events. Using Tracer, describe how changing the cladogenesis prior affects the extinction rate when compared with the "common rate" model.
- How would you constraint the rate matrix to allow ranges of size two at largest.
- (1 of 2) Saving your commands to a file, create a script to produce the "per-area" rate model.
- (2 of 2) Determine if the data support the "common rate" model over the "per-area" rate model. Use the stepping stone method to compute marginal likelihoods, which will let you compute Bayes factors for model selection (see Section XXX).
- (Advanced) Using what you learned in this tutorial and the CTMC tutorial (Section XXX), perform a joint analysis of molecular and biogeographic evolution for primates. Introduce a common prior for the molecular and biogeographical clocks, e.g.

```
clock_mol      ~ dnExp(10.)
clock_scale_bg ~ dnGamma(2.,2.)
clock_bg       := clock_mol * clock_scale_bg
```

3 Epoch models and ancestral state reconstruction

4 Large numbers of areas

4.1 Data augmentation

For small rate matrices, transition probabilities of beginning in state i and ending in state j equal the matrix exponential of the underlying rate matrix, scaled by the elapsed time of the process. This integrates over all unobserved transition events during the time interval t. Unfortunately, computing the matrix exponential scales poorly as the state space increases, i.e. $O(n^4)$ for n states.

Alternatively, the probability of beginning in state i and ending in state j can be computed easily when the explicit series of event types and times are known. While we will never know the exact history of events, we can use stochastic mapping in conjunction with Markov chain Monte Carlo (MCMC) to repeatedly sample range evolution histories that are consistent with the ranges observed in the study taxa at the tips of the phylogeny. This technique is called data augmentation, and was first applied in phylogenetics to tertiary structure-dependent evolution of protein-coding nucleotide sequences (**?**).

This is the strategy we will use to infer the posterior distribution approximated by
$\text{Prob}(\mathbf{X}_{aug}, \theta \mid \mathbf{X}_{obs}, T, M)$, where $\mathbf{X}_{obs}$ is the range data observed at the tips, $\mathbf{X}_{aug}$ is the distribution of ancestral range reconstructions over the phylogeny, T, where $\mathbf{X}_{aug}$ is inferred jointly with the parameters, θ, assuming the range evolution model, M, that describes $\mathbf{Q}$ above. Ancestral range reconstructions are often of primary interest in phylogenetic biogeographic analyses, which are generated as stochastic mappings with support values as a by-product data augmentation.

You may wonder why matrix exponentiation works fine for molecular substitution models and large multiple sequence alignments. Molecular substitution models typically assume each site in the multiple sequence alignment evolves independently, which may be justified because recombination degrades linkage disequilibrium over geological timescales. Conveniently, this keeps $\mathbf{Q}$ small even for datasets with many sites.

4.2 Large rate matrices

This matrix can be represented compactly as the rate function

$$q^{(a)}_{\mathbf{y},\mathbf{z}} = \begin{cases} \lambda_0 & \text{if } z_a = 0 \\ \lambda_1 & \text{if } z_a = 1 \\ 0 & \mathbf{y} \text{ and } \mathbf{z} \text{ differ in more than one area} \end{cases} .$$

where $\mathbf{y}$ and $\mathbf{z}$ are the "from" and "to" ranges and a is the area that changes. For example, $q^{(1)}_{011,111}$ is the rate of range expansion for $011 \rightarrow 111$ to gain area 1. Note the rate of more than one event occurring simultaneously is zero, so a range must expand twice by one area in order to expand by two areas. This model is analogous to the Jukes-Cantor model for three independent characters with binary states, except the all-zero "null range" is forbidden.

4.3 Distance-dependent dispersal function

Lastly, we may reasonably expect that a range expansion event into an area depends on which nearby areas are currently inhabited, which imposes non-independence between characters. The transition rate might

then appear as

$$q^{(a)}_{\mathbf{y},\mathbf{z}} = \begin{cases} \lambda_0 & \text{if } z_a = 0 \\ \lambda_1 \eta(\mathbf{y}, \mathbf{z}, a, \beta) & \text{if } z_a = 1 \\ 0 & \mathbf{y} = 00...0 \\ 0 & \mathbf{y} \text{ and } \mathbf{z} \text{ differ in more than one area} \end{cases} .$$

For this tutorial, you can take $\eta(\cdot)$ to adjust the rate of range expansion into area a by considering how close it is to the current range, $\mathbf{y}$ relative to the closeness of all other areas unoccupied by the taxon. The β parameter rescales the importance of geographic distance between two areas by a power law. Importantly, $\eta(\cdot) = 1$ when $\beta = 0$, meaning geographic distance between areas is irrelevant. Moreover, when $\beta > 0$, $\eta(\cdot) < 1$ when area a is relatively distant and $\eta(\cdot) > 1$ when area a is relatively close. See **?** for a full description of the model.

4.4 Specifying a data augmented DEC model

As previously, start by setting your working directory,

```
setwd("/Users/arwallace/projects/RB_Biogeography_tutorial/")
```

then create helper variables for file handling,

```
fp      = "./"
area_fn = fp + "data/earth25.still.atlas.txt"
data_fn = fp + "data/primates_bg_n25.nex"
tree_fn = fp + "data/primates.tree"
out_str = "bg_3"
```

read in our tree,

```
tree <- readTrees(in_fp + data_fn)[1]
```

populate our range observations,

```
data    = readDiscreteCharacterData(in_fp + data_fn)
```

and read in our geographical information (for details, see Section XX).

```
atlas  = readAtlas(in_fp + area_fn)
n_areas = atlas.nAreas()
```

Lastly, create index variables to populate our move and monitor vectors,

```
mvi = 1
mni = 1
```

and assign the number of generations to run the MCMC analysis

```
ngen = 500000
```

To later interpret ancestral state monitors phylogenetically, save a copy of `tree` annotated with internal node indexes.

```
write(tree,filename=tree_fn+".index.tre")
```

Proceeding with the model configuration, we'll first create our rate matrix that determines the rate of per-area gain and loss given the current geographical layout of the range. In RevBayes, data-augmented CTMC analyses require `RateMap` functions to determine event rates, which differ from the familiar `RateMatrix` functions that include `fnJC` and `fnGTR` as members. In their simplest form, `RateMap` functions generate the rates of change over the full set of characters, where each character evolves according to a provided `RateMatrix` function. Additionally, a `RateMap` accepts a rate modifier function that induces some correlation structure to character change evolution. In this section, we'll be creating a biogeographic `RateMap` function for the dispersal-extinction process given above.

First, create a biogeographical clock to scale the rate of range evolution.

```
clock_bg ~ dnExp(10)
moves[mvi++] = mvScale(clock_bg, lambda=0.5, weight=5.0)
```

Next, instantiate a simplex of gain and loss rates, distributed by a flat Dirichlet prior,

```
glr ~ dnDirichlet([1,1])
moves[mvi++] = mvSimplexElementScale(glr, alpha=30.0, weight=5.0)
```

and use deterministic nodes to assign the rates nicknames.

```
r_gain := glr[1]
r_loss := glr[2]
```

Insert the simplex into the rate matrix q_area, which gives the average rate of area gain and loss per area.

```
q_area := fnFreeBinary(glr)
```

Next, we will create `dp` to represent the β parameter, which determines the importance of geographical distance to dispersal. Remember that values of β far from zero means distance is important. So, if we we assign a prior that pulls β towards zero, then posterior values of β far from zero indicate the range data are informative of the importance of distance to dispersal. We'll use an exponential distribution with mean 1.0 as a prior for `dp`.

```
dp ~ dnExponential(10.0)
moves[mvi++] = mvScale(x=dp, lambda=0.5, tune=true, weight=5.0)
```

We will also create a deterministic node to modify the rate of dispersal between areas by evaluating `dp` and `atlas`. This node is determined by the function `fnBiogeoGRM`, where GRM stands for "geographical rate modifier", and plays the role of the $\eta(\cdot)$ rate-modifier function mentioned earlier. We will tell the `fnBiogeoGRM` function to modify dispersal rates based on distances and whether or not the area exists during an epoch.

```
grm := fnBiogeoGRM(atlas=atlas, distancePower=dp, useDistance=true)
```

Now we need a deterministic node to represent the rate matrix, **Q**. To determine the value of this node, we'll use the function `fnBiogeoDE` to assign our model parameters to transition rates as described in the introduction. As input, we'll pass our gain and loss rates, `q_area`, our geographical rate modifier, `grm`, and the biogeographical clock `clock_bg`. In addition, we'll inform the function of the number of areas in our analysis and whether we will allow species to be absent in all areas (i.e. have the null range).

```
q_range := fnBiogeoDE(gainLossRates=q_area, branchRates=clock_bg, geoRateMod=grm,
   numAreas=n_areas, forbidExtinction=true)
```

As with the simple DEC model, we assign a flat Dirichlet prior over cladogenic event type probabilities

```
clado_prob ~ dnDirichlet( [1, 1, 1] )
widespread_sympatry := clado_prob[1]
subset_sympatry   := clado_prob[2]
allopatry         := clado_prob[3]
moves[mvi++] = mvSimplexElementScale(clado_prob, alpha=20.0, weight=5.0)
```

Finally, the data evolve according to a phylogenetic CTMC process. Here, we decalre a stochastic node using `dnPhyloDACTMC` where `DA` indicates the distribution requires data augmentation to compute the

likelihood rather than Felsenstein's pruning algorithm. To create the distribution, we must pass it our `tree` and `q_range` objects, but additionally inform the distribution that it will be using a biogeographic model, that it will introduce the simple cladogenic range evolution events described in **?** (`useCladogenesis=true`), and that it will assign zero probability to a transition away from the null range state.

```
m ~ dnPhyloDACTMC(tree=tree, Q=q_range, cladoProbs=clado_prob, type="Biogeo",
    forbidExtinction=true, useCladogenesis=true)
```

So we may evaluate the graphical model's likelihood, we tell the CTMC to observe the `data` object, which then primes the model with data-augmented character histories. Now `m` has a defined likelihood value.

```
m.clamp(data)
m.lnProbability()
   -156.0288
```

To integrate over the space of possible range histories, we still need to add moves to propose new data augmented histories. The major challenge to sampling character histories is ensuring the character histories are consistent with the observations at the tips of the tree. The proposals in this tutorial use **?**'s rejection sampling algorithm, with some modifications to account for cladogenic events and epoch-based rate matrices.

The basic idea is simple. Each time a character history proposal is called, it selects a node at random from the tree. Branch history proposals propose a new character history to a single randomly-chosen branch. Node history proposals propose a new character history for the three branches connecting to a randomly chosen node, in addition to the cladogenic state of the node itself.

For each proposal, each character's history is resampled with probability `lambda` – i.e. `lambda=0.01` resamples 1% of characters, while `lambda=1.` resamples all characters. Once the new character history is proposed, the likelihood of the model is evaluated and the MCMC accepts or rejects the new state according to e.g. the Metropolis-Hastings algorithm.

Cladogenic events require special considerations during sampling, so we indicate `type="Biogeo"`. Currently, only rejection-sampling is available for cladogenic histories, hence `proposal="rejection"`. Finally, we apply high `weight` values to the proposals since the larger the state space is, the more character history proposals needed to effectively integrate over the space of sample paths.

Let's create the character history moves as follows: conservative character history updates for paths and nodes, with `lambda=0.05`

```
moves[mvi++] = mvCharacterHistory(ctmc=m, qmap=q_range, tree=tree, lambda=0.05, type="
    Biogeo", graph="node", proposal="rejection", weight=100.0)
moves[mvi++] = mvCharacterHistory(ctmc=m, qmap=q_range, tree=tree, lambda=0.05, type="
    Biogeo", graph="branch", proposal="rejection", weight=100.0)
```

and the same proposals for more radical character history updates, with `lambda=1.0`

```
moves[mvi++] = mvCharacterHistory(ctmc=m, qmap=q_range, tree=tree, lambda=1.0, type="
    Biogeo", graph="node", proposal="rejection", weight=40.0)
moves[mvi++] = mvCharacterHistory(ctmc=m, qmap=q_range, tree=tree, lambda=1.0, type="
    Biogeo", graph="branch", proposal="rejection", weight=40.0)
```

Next, create the model object,

```
my_model = model(m)
```

and monitors for our simple parameters.

```
monitors[mni++] = mnScreen(clock_bg, r_gain, r_loss, dp, subset_sympatry, allopatry,
    widespread_sympatry, printgen=100)
monitors[mni++] = mnFile(clock_bg, r_gain, r_loss, dp, subset_sympatry, allopatry,
    widespread_sympatry, filename=out_fn+".params.txt", printgen=10)
```

Like any parameter, we can sample the augmented range histories from the MCMC to approximate the posterior distribution of range histories. This is statistically equivalent to generating ancestral state reconstructions from a posterior distribution via stochastic mapping. We will extract these reconstructions using special monitors designed for the `dnPhyloDACTMC` distribution.

Next, we will create `mnCharHistoryNewick` monitors to record the sampled character history states for each node in the tree. This monitor has two `style` options: `counts` reports the number of gains and losses per branch in a tab-delimited Tracer-readable format; `events` reports richer information of what happens along a branch, anagenically and cladogenically, using an extended Newick format. How to read these file formats will be discussed in more detail in Section **??**.

```
monitors[mni++] = mnCharHistoryNewick(filename=out_fn+".events.txt", ctmc=m, tree=tree,
    printgen=100, style="events")
monitors[mni++] = mnCharHistoryNewick(filename=out_fn+".counts.txt", ctmc=m, tree=tree,
    printgen=100, style="counts")
```

As our last monitor,`mnCharHistoryNhx` records character history values throughout the MCMC analysis, then stores some simple posterior summary statistics as a Nexus file. These summary statistics could be computed from the previously mentioned monitor output files, but `mnCharHistoryNhx` provides a simple way to produce Phylowood-compatible files. We will also discuss this file's format in more detail later in the tutorial.

```
monitors[mni++] = mnCharHistoryNhx(filename=out_fn+".phw.txt", ctmc=m, tree=tree, atlas=
    atlas, samplegen=10, maxgen=ngen, burnin=0.5)
```

Finally, create the MCMC object

```
my_mcmc = mcmc(my_model, monitors, moves)
```

and run

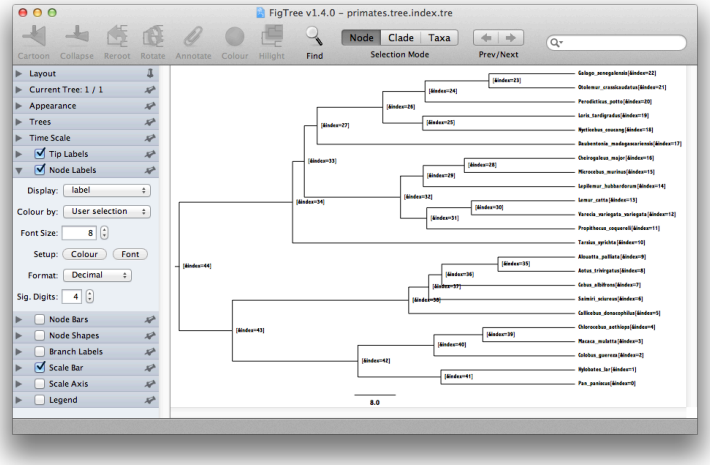
```
my_mcmc.run(generations=ngen)
```

4.4.1 Exercises

- How sensitive are the rates of area gain and loss to the prior distribution on `dp` (β)?

4.5 Analysis output

You will need a node-indexed phylogeny to interpret ancestral state reconstructions. First, open FigTree and load the Newick tree stored in `data/primates.tree.index.tre`. Expand "Node Labels" and change "Display" to the custom node label. All sampled characters have a node index, which corresponds to the branch ancestral to the indexed node.



We'll focus some attention on node 42, the most recent common ancestor of chimps and macaques, designated as the Old World most recent common ancestor (MRCA).

4.5.1 Biogeographic event counts from `mnCharHistoryNewick`

Recording stochastic mappings in a Tracer-compatible format requires some summarization. This monitor generates a tab-delimited file where the number of events of each type for each branch is recorded.

Open `./output/bg_3.counts.txt` in a text editor.

```
Iter    Posterior  Likelihood Prior  t_s0   t_s1   t_c0   t_c1   t_c2   t_c3   b0_s0
      b0_s1  b0_c   ...
0   -6518.54   -6519.25   0.706823   977 839 22 0   0   0   38  28  0   ...
10  -583.147   -585.333   2.186240   66  37  3   7   9   3   2   1   2   ...
20  -296.540   -297.340   0.799755   20  25  15  1   3   3   0   1   0   ...
30  -276.284   -277.257   0.972918   17  24  14  0   4   4   0   1   0   ...
40  -266.569   -266.948   0.379624   18  23  15  1   3   3   0   1   3   ...
...
```

For example, `b0_s1` gives the number of areas that are gained for the branch leading to the node indexed 0. Referencing FigTree, we see this corresponds to chimpanzees. `b0_c` gives the cladogenic event type that gives rise to the chimp lineage, where narrow sympatry, widespread sympatry, subset sympatry, and allopatry are recorded as `0`, `1`, `2`, and `3`, respectively. The columns `t_s0` and `t_s1` give the sum of events over all branches. `t_c0`, `t_c1`, `t_c2`, and `t_c3` give the total number of narrow sympatric, widespread sympatric, subset sympatric, and allopatric cladogenic events over the entire tree.

4.6 Biogeographic event histories from `mnCharHistoryNewick`

For more detailed data exploration, this analysis also provides annotated Newick strings with the complete character mappings for the tree. (This file format is a bit unwieldy and under revision.)

→ Open `./output/bg_3.events.txt` in a text editor.

Each iteration records the data-augmented character history (stochastic mapping) using metadata labels, which, for an internal node, looks like

```
[&index=42;nd=0000000000000101000000000;pa=0000000000000100000000000;ch0
   =0000000000000101000000000;ch1=0000000000000001000000000;cs=s;bn=41;ev={{t:0.138033,
   a:39.4458,s:1,i:15}}]
```

Having consulted FigTree earlier, we know node 42 is the Old World MRCA. The branch began with the range `pa=0000000000000100000000000` and terminated in the state `nd=0000000000000101000000000`. Since this node is not a tip node, it represents a speciation event, so the daughter ranges are also given, `ch0=0000000000000101000000000` and `ch1=0000000000000001000000000`. The cladogenic state for this speciation event was subset sympatric, `cs=s`, rather than sympatric (wide or narrow; `w` or `n`) or allopatric (`a`).

Anagenic dispersal and extinction events occurring along the lineage leading to node 42 are recorded in `ev`, where each event has a time (relative to the absolute branch length), absolute age, state (into), and character index (`t`, `a`, `s`, `i`, resp.). Potentially, `ev` contains multiple events. For this posterior sample, the MRCA of chimps and macaques dispersed into East Africa 39.4458 million years ago, which is consistent with the ranges recorded by `pa` and `nd`.

Although we have stochastic mappings under the posterior distribution, the remaining challenge is to summarize them into something useful. The Python script `bg_parse.py` is provided to manipulate this data format. Below are a few examples of interesting features of the posterior.

→ Open a Python console and read in the events.

```
> cd RevBayes_scripts
> python

...

>>> from bg_parse import *
>>> d=get_events(fn="../output/bg_3.events.txt")
```

By default, `get_events()` extracts a dictionary-of-dictionaries from the posterior event samples. The first key corresponds to the node (branch) whose MCMC samples you'd like to retrieve, while the second dictionary's keys are the columns correspond to MCMC states and values specific to that node. For example, say we are interested in the last five cladogenic states sampled for node 42, Old World MRCA,

```
>>> dd[42].keys()
['ch1', 'iteration', 'bn', 'nd', 'ch0', 'prior', 'posterior', 'pa', 'cs', 'ev', '
   likelihood']
>>> dd[42]['cs'][-5:]
['widespread_sympatry', 'widespread_sympatry', 'widespread_sympatry', '
   widespread_sympatry', 'widespread_sympatry']
```

To get the `n=1` highest-valued sample for a branch by its posterior value

```
>>> get_best(dd[42],n=1,p='posterior')
{'prior': [-0.524716], 'iteration': [46700], 'bn': [41], 'nd': [[0, 0, 0, 0, 0, 0, 0, 0,
    0, 0, 0, 1, 0, 1, 0, 1, 0, 0, 0, 0, 0, 0, 0, 0, 0]], 'ch0': [[0, 0, 0, 0, 0, 0, 0,
   0, 0, 0, 0, 1, 0, 1, 0, 1, 0, 0, 0, 0, 0, 0, 0, 0, 0]], 'ch1': [[0, 0, 0, 0, 0, 0,
   0, 0, 0, 0, 0, 1, 0, 1, 0, 1, 0, 0, 0, 0, 0, 0, 0, 0, 0]], 'posterior': [-95.7676],
   'pa': [[0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 1, 0, 1, 0, 1, 0, 0, 0, 0, 0, 0, 0, 0, 0]],
    'cs': ['widespread_sympatry'], 'ev': [[]], 'likelihood': [-95.2429]}
```

More data-exploration functions are found in `bg_parse.py`.

4.7 Phylowood animation file (`./output/bg_3.nhx.txt`)

Because this data is very high-dimensional, we'll use an external data exploration tool to look at range evolution.

This file summarizes the MCMC output from a RevBayes biogeographical analysis as a Nexus-formatted file. The `geo` block gives the geographical latitudes and longitudes for the areas in the order they are reported as probabilities. Like the `my_run.area_probs.txt` file, this file is not written until the analysis is complete. This annotation is used for the two visualization programs covered in the next section, Phylowood and BayArea-Fig. The anatomy of the Phylowood and BayArea-Fig settings blocks will also be explained there.

5 Visualization

Here we'll explore two options for visualizing ancestral range reconstructions. I'll walk you through some of the basic functionality, but feel free to play around as you like.

5.1 Phylowood

Phylowood generates interactive animations to explore biogeographic reconstructions.

→ Open `http://mlandis.github.io/phylowood`.

→ Drag and drop `./output/bg_2rate.nhx.txt` into the text field.

→ Click the Play button to view the animation.

There are three control panels to help you filter data: the media panel, the map panel, and the phylogeny panel. The media buttons correspond to Beginning, Slow/Rewind, Play, Stop, Fast Forward, Ending (from left to right). The animation will play the timeframe corresponding to the slider.

→ Drag the slider to the right (the present).

→ Pan and zoom around the map.

Marker colors correspond to the phylogenetic lineages in the phylogeny panel. Markers are split into slices and (loosely) sorted phylogenetically, so nearby slices are generally closely related. At divergence events, a marker's radius is proportional to the marginal posterior probability the node was present in the area at that time. Between divergence events, marker's radius is simply an interpolation of the values at the two endpoints. Some information about geological constraints and cladogenic events is lost.

→ Mouseover an area to learn which lineage it belongs to and its presence probability.

Since it's difficult to see how specific clades evolve with so many taxa, Phylowood offers two ways to filter taxa from the animation. We call the set of a lineage, all its ancestral lineages towards the root, and all descendant lineages a phylogenetic heritage. The root's heritage is the entire clade. A leaf node's heritage

is a path from the tip to the root.

→ Mouseover a lineage to temporarily highlight the lineage's heritage. Remove the mouseover to remove the highlight effect.

The highlight effect is temporary and quickly allows you to single out lineages of interest during animation. Phylowood also offers a masking effect that persists until an unmask command is issued.

→ Double-click the white root branch to mask the root node's heritage (all lineages). Single click a lineage to unmask that lineage's heritage.

Now that the masking effects are in place, you're free to interact with other map components. In addition, the area of marker sizes is only distributed among unmasked lineages.

→ Visit `https://github.com/mlandis/phylowood/wiki` to learn more about Phylowood.

Version dated: February 3, 2015

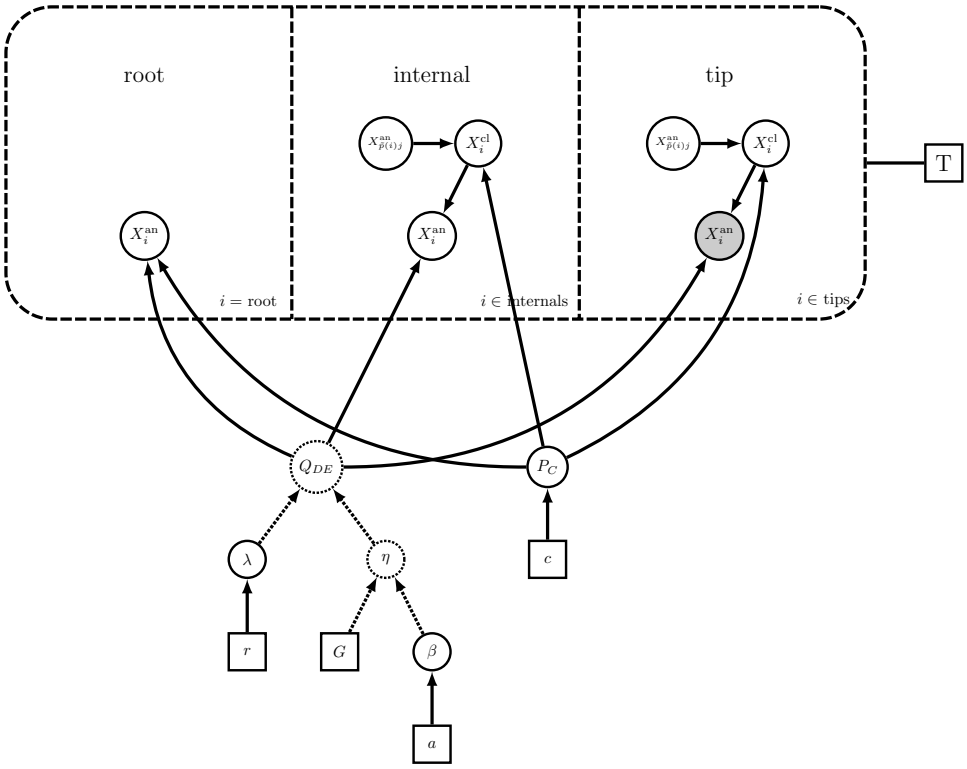


Figure 1: Graphical model of DEC. The tree plate's topology is fixed by T, where each internal node has both an anagenic and cladogenic random variable (X_i^{an} and X_i^{cl}, resp.) that represents an ancestral species before and after it speciated. Anagenic change is modeled by a continuous time Markov process, where Q_{DE} is the instantaneous rate matrix of area gain and loss, as parameterized by λ. The geographic distance rate modifier function, η, takes in the geographical distances and strata as G, and the distance power parameter, β. Cladogenic change is modeled by P_C, a Dirichlet-distributed simplex with a flat prior.

Figure 2: Phylowood frame showing posterior ancestral range of root node.

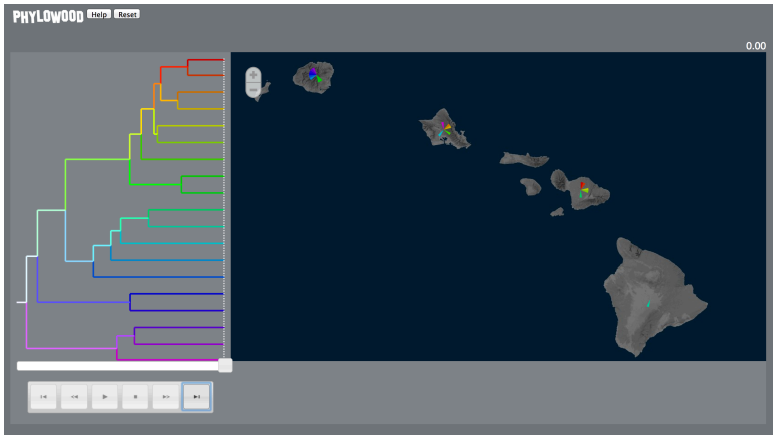


Figure 3: Phylowood frame showing distribution of extant taxon ranges.

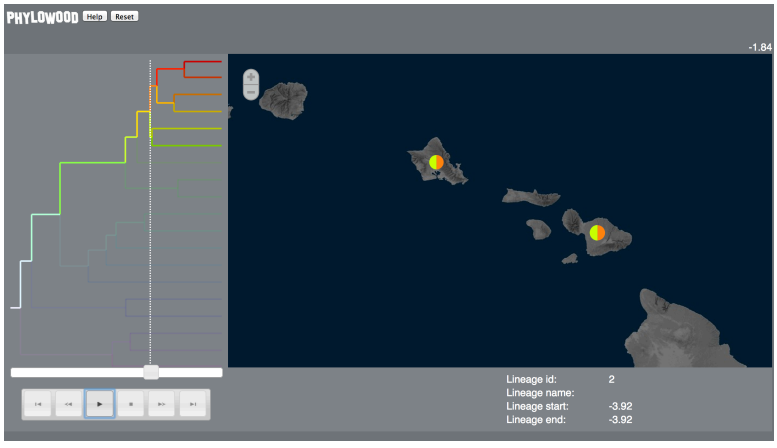


Figure 4: Phylowood frame highlighting the posterior range for the most recent common ancestor of *P. mauiensis* and *P. hawaiiensis*.