

Introduction

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INTRODUCTION

Once upon a time, there was the evolutionary history of all life on Earth. Let me tell the simplified version of this story and how to put this into figures called phylogenies, before moving to the more complex details. The formation of the Earth began approximately 4.5 billion years ago (Dalrymple 2001). From an evolutionary biologists' point of view, this was a dull time, until the first living organism appeared.

This First Universal Common Ancestor (FUCA) came into existence at least 3.48 billion years ago (Noffke *et al.* 2013). FUCA may not have been alone, but these other early life forms went extinct¹ and are ignored in this story anyways. We can depict the evolutionary history of FUCA at that point in time with figure 1.1.

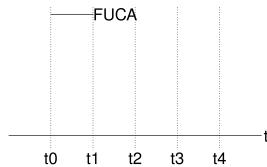


Figure 1.1 | Evolutionary history of the First Universal Common Ancestor (FUCA). Time goes from past (left) towards the present (right).

One unknown day, the descendants of FUCA became dissimilar enough to say that the one species called FUCA has given rise to two species (note the difficulty in determining what a species is at that time!). This event doubled the biodiversity on Earth. The two species that FUCA has evolved into, we will call species A and B. Species A and B are sister species. We can depict the evolutionary history of FUCA as seen in figure 1.2.

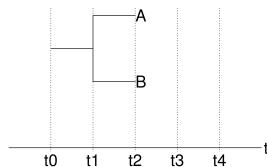


Figure 1.2 | Evolutionary history of the two descendants of FUCA. Time goes from past (left) towards the present (right).

Both species A and B had their unknown histories. They may have gone extinct themselves, as extinction is a common event: it is estimated that more than 99% of all species that has ever lived on Earth has gone extinct (Newman 1997). Alternatively, they gave rise to new species, but also these are just as likely to go extinct. For this story, we will assume A and/or its clade went extinct and that species B created a sister species C. Species B and C will give rise to all contemporary biodiversity. This ancestor of species B and C is called the Last Universal Common Ancestor, or LUCA. LUCA is estimated to have lived between 3.48 (Noffke *et al.* 2013) and 4.5 (Betts *et al.* 2018) billions of years ago. We can depict the evolutionary history of FUCA as seen in figure 1.3. Here, billions of years ago, is where the story ends and we will move on to the present.

¹by definition!

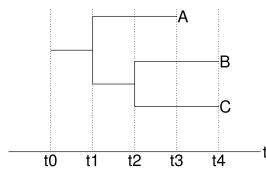


Figure 1.3 | Evolutionary history of the three descendants of FUCA, of which one went extinct. Assuming B and C will give rise to all contemporary biodiversity, the Last Universal Common Ancestor (LUCA) must have come into existence at timepoint t1. Time goes from past (left) towards the present (right).

The idea that all life on Earth is related was first posed by Charles Darwin in his book 'On the Origin of Species' in 1859 (Darwin 1859). His first sketch of an evolutionary tree is shown in figure 1.4.

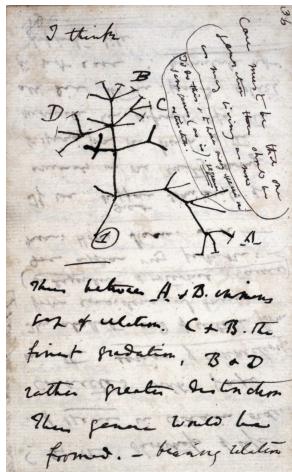


Figure 1.4 | Charles Darwin's 1837 first sketch of an evolutionary tree

The biodiversity derived from the first life on Earth is important to us humans (apart from that it has created us) for many reasons. In its own, biodiversity is found so important, that, for example, the European Union has an explicit Biodiversity Strategy, which aims to halt the loss of biodiversity (see https://ec.europa.eu/environment/nature/biodiversity/strategy/index_en.htm). Biodiversity usually improves ecosystem services (Cardinale *et al.* 2012), where ecosystem services are features of biological systems that are positive for human well-being, for example food, carbon sequestration, waste decomposition and pest control. Therefore, biodiversity is linked to human well-being.

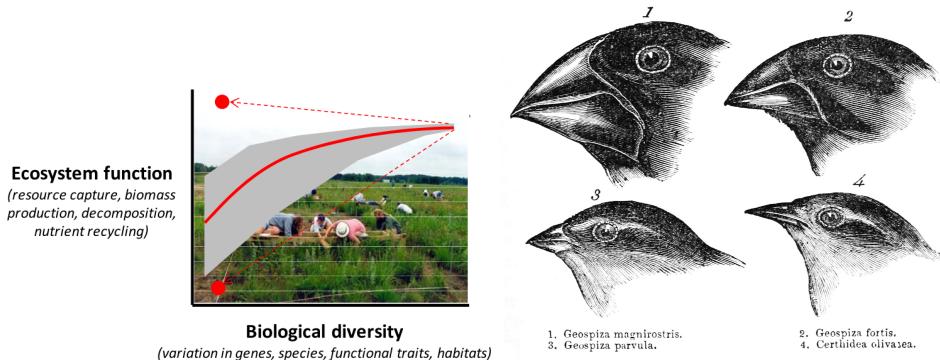


Figure 1.5 | Left: a diversity-function relationship found to be typical from hundreds of studies. The red line represents an average, where the grey polygon represents a 95% confidence interval. The red dots show the lower and upper limit for monocultures. From Cardinale *et al.* 2012. Right: Darwin's finches, by John Gould.

Speciation is the process that increases biological diversity. This process is studied from multiple angles, among others, we can study the mechanism ('what causes a speciation event?') or we can study the patterns of many of such events ('is speciation rate constant through time?'). Darwin's finches (see figure ??) are an iconical example with 25 thousand results on Google Scholar. The mechanism of a speciation event already has many facets and can be caused by geographical isolation (e.g. Mayr 1942), ecological factors (e.g. Lack 1947) and more, yet listing and explaining all mechanisms is beyond the scope of this thesis.

One way to study speciation is to look at patterns of speciation events through evolutionary time. For this, we need to have a phylogeny (note that getting such a phylogeny is hard, see below). From a phylogeny, we can ask many question such as 'How often do speciation and extinction events take place?' 'Are speciation and extinctions rates constant, or do they change?', 'What causes a change in speciation or extinction rate?' or 'Is there an upper limit on the number of species?'. There are two methods to research speciation patterns back in evolutionary time: the use of fossils or using molecular phylogenies.

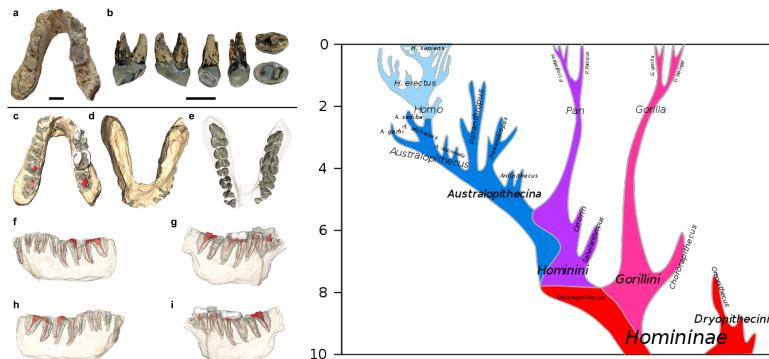


Figure 1.6 | Left: El Graeco fossil, from Fuss *et al.* 2017. Right: Evolution of the Homininae, based on Stringer 2012

Using fossils is a classic way to look back in evolutionary time. Fossils show a glimpse of the biodiversity in the past. We can deduce the age of fossils, by the rock layers they are found in. Using fossils has its limitations. First, it is mostly species with hard body parts that are suitable to fossilize. Of such species, an organisms is still only rarely preserved, of which only a fraction under ideal circumstances. Of these fossils, only a fraction is discovered. One example of a famous fossil is 'El Graeco', which may be the oldest known hominin (Fuss *et al.* 2017), where hominins are the tribe (taxonomic group) we Homo sapiens share with the Panini.

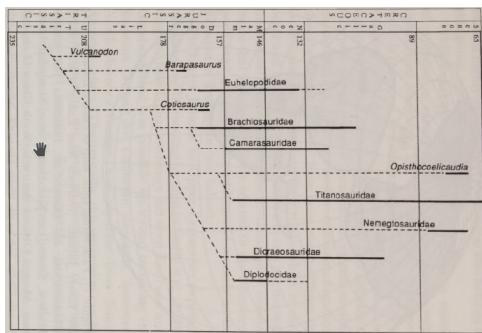


Figure 1.7 | The evolutionary history of sauropod dinosaurs, from Upchurch 1995

Using molecular phylogenies is the modern way to look back in evolutionary time. It is the use of heritable molecules (for example DNA, RNA, or protein) of contemporary species to infer phylogenies. The field of phylogenetics is the research discipline that intends to infer the most accurate phylogenies possible, regarding topology, speciation and extinction times, optionally adding morphological data and/or fossil data. Phylogenetics is applied in many settings, among others, species classification, forensics, conservation ecology and epidemiology (Lam *et al.* 2010).

One example of the importance of an accurate phylogenetic tree is demonstrated in Bush *et al.* 1999. This study investigated which loci of the H3 hemagglutinin surface protein are under selection, by contrasting nonsynonymous and synonymous mutation rates along the branches of a phylogeny. In a preliminary analysis by the authors, they noted that most selection rates were either below or above the statistical threshold depending on the phylogeny. This study contributed to the selection of recommended composition of influenza virus vaccines.

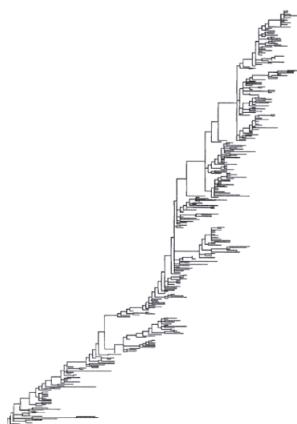


Figure 1.8 | Phylogeny of the human influenza virus type A subtype H3, from Bush *et al.* 1999

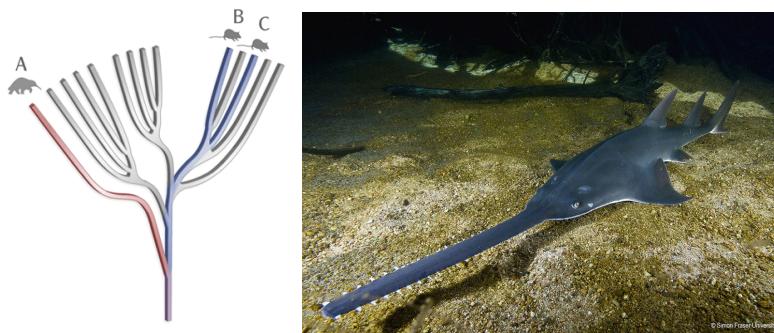


Figure 1.9 | Left: The ED (evolutionary distinctiveness) of species A is higher than that of species B or C, as more evolutionary history will be lost when that species goes extinct. Right: The Largetooth Sawfish (*Pristis pristis*) is at number 1 of the EDGE (ED = 'Evolutionary Distinctiveness', GE = Globally Endangered status) list, with an EDGE Score of 7.38 and an ED of 99.298.

Another example of the importance of an accurate phylogenetic tree comes from conservation biology, in which phylogenies are used to calculate an EDGE ('Evolutionarily Distinct and Globally Endangered') score. Species with a high EDGE score are prioritized in conservation. To calculate an EDGE score, one needs a metric of evolutionary distinctiveness ('ED') and globally 'endangeredness' ('GE'). The GE score is a conservational status, ranging from zero ('Least Concern') to four ('Critically Endangered'). The ED embodies the amount of evolutionary history lost when a species would go extinct, which can be calculated from a (hopefully accurate) phylogeny.



Figure 1.10 | PHYLIP logo

Phylogenetics has taken a huge flight, due to the massively increased computational power and techniques. A first milestone in this file is Felsensteyn's work in 1980, creating (and still maintaining!) PHYLP, the first software package for classical phylogenetic analysis. Another milestone is the Metropolis-Hastings algorithm, which allowed Bayesian phylogenetics to thrive, resulting in contemporary tools such as BEAST, BEAST2 (of which more below), MrBayes and RevBayes.



Figure 1.11 | BEAST2 logo (left) and example output (right)

A clear example of the power of modern phylogenetics, is the Tree Of Life: it uses 3,083 genomes of 2,596 amino-acid positions to create one big phylogeny of all (sequenced) life on Earth, which took 3,840 computational hours on a modern supercomputer (Hug *et al.* 2016).

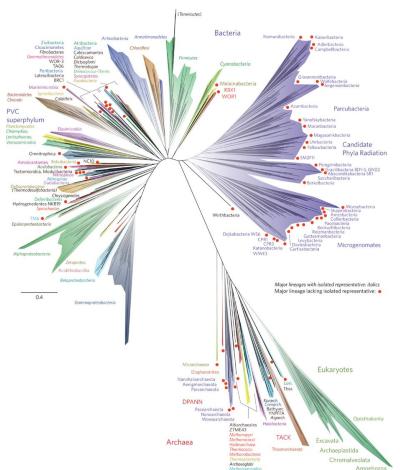


Figure 1.12 | Tree of Life, from Hug *et al.* 2016

To create such a tree from protein sequences, one has to specify an evolutionary model. This evolutionary model embodies our set of assumptions, such as the evolution of a protein sequence (also called the site model), the rate(s) at which this happens (the clock model) and the rate(s) at which a branching/speciation event takes place (the tree model). For example, the amino acids of the Tree Of Life are assumed to change/mutate according to the LG model (Le & Gascuel 2008), which is a model that uses the average transition rates found in nature.

There are many evolutionary models to choose from, and selecting which one to use

is hard, due to the many sets of assumptions to choose from. In general, modellers are looking for that set of assumptions that is as simple as possible, but not simpler. And even then, sometimes an overly simplistic model is picked regardless, due to computation constraints.

By using a model comparison, one has a rational way to select an evolutionary model that is as simple as possible, but not simpler. A model comparison algorithm selects the evolutionary model that is most likely to have generated the data, without being overly complex. The idea is that the best evolutionary model should result in the most accurate phylogenetic trees.

Because model comparison is hard, there have been multiple studies that investigate the effect of picking the wrong evolutionary models.

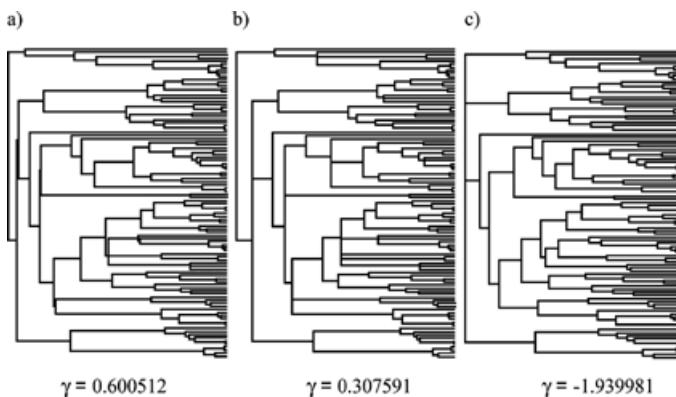


Figure 1.13 | Figure from Revell *et al.* 2005. At the left was the true tree. In the middle the inferred tree, that used the generative model At the left the inferred tree when using a too simple inference model

One example that demonstrates the effect of using a too simple inference model comes from Revell and colleagues (Revell *et al.* 2005). They simulated many phylogenies and respective DNA sequences using different DNA substitution models. After this, they inferred phylogenies from the simulated alignments with either the correct or a simpler DNA substitution model. Ideally, the inferred phylogenies match the phylogenies the alignments are based upon. They found that when the DNA model is the correct one, inference of the phylogenies is satisfactory. However, when using an overly simplistic DNA model, the inferred trees show a slowdown in their speciation rates, even when the original trees were simulated with a constant speciation rate. This study shows that a decreasing speciation rate may be attributed to an overly simplistic DNA model, instead of an interesting biological process.

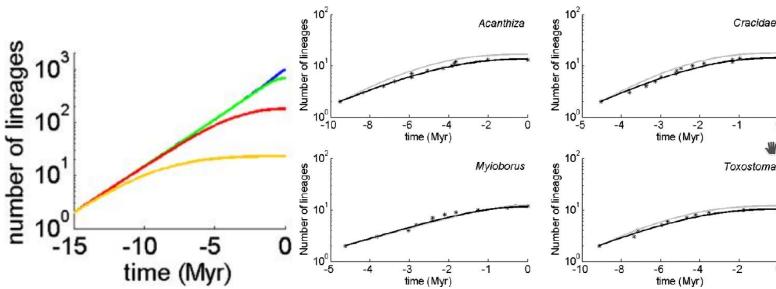


Figure 1.14 | Left: example lineage-through-time plots, for different speciation completion rates: yellow = 0.01, red = 0.1, green = 1.0, blue = 10. Note the slowdown in the accumulation of new lineages when speciation completion rate is lowered. Right: number of species through time plots for four bird phylogenies, (after Phillipmore & Price 2008) Both figures are adapted from Etienne & Rosindell 2012

A more recent example that demonstrates the effect of using an overly simple inference model is about assuming a wrong clock model. A clock model embodies our assumptions regarding the mutation rates in the history of different taxa. The simplest clock model, called the strict clock model, assumes these mutation rates are equal across all taxa. Using a wrong clock model has a profound impact on the inferred phylogenetic trees, unless we can specify the timing of some early speciation events (Duchêne *et al.* 2014).

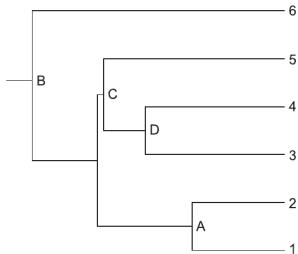


Figure 1.15 | Phylogeny with speciation events labelled A to D, where B is the earliest speciation event. Figure from Duchêne *et al.* 2014.

The tree model is the most important piece of an evolutionary model, with regard to speciation. The assumptions of a tree model is called the tree prior, where 'prior' refers to the knowledge known before creating a phylogeny. The tree prior specifies how likely processes that determine the shape of a tree occur. These two processes are (1) the formation of a new branch, and (2) the termination of an existing branch. In the context of speciation, we call these two events a speciation and an extinction event respectively.

There are two standard tree models, called the Yule and Birth-Death model. The most basic speciation model is the Yule model (Yule 1925), which assumes that speciation is constant and there is no extinction. Albeit that extinction is a well-established phenomenon, the use of the Yule model is its simplicity: it is the simplest evolutionary model to work with, and the computation of its different aspects is fastest, making it a good first stop in an evolutionary experiment. Similar to the simplest models of bacterial growth, the Yule model predicts that the number of species grows exponentially through

time. Because the Yule model would later be classified as a Birth-Death model without extinction, it is nowadays also called the Pure-Birth model.

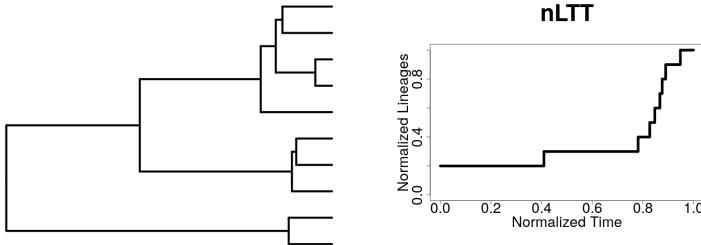


Figure 1.16 | Left: An example Yule tree Right: A lineages-through-time plot of the example Yule tree. In all cases, time goes from past (left) towards the present (right).

The Birth-Death model (Nee S., May R. M. & Harvey P. H. 1994) is an extension of the Yule model, as it adds an extinction rate. Similar to the constant birth rate, the extinction rate is assumed to be constant as well. As a consequence, the BD model predicts two outcomes: if the speciation rate exceeds the extinction rate, the number of extant species grows exponentially through time. The other way around, however, when the extinction rate exceeds the speciation rate, the number of lineages is expected to decline exponentially. It is clear that an exponential growth in the expected number of lineages is biologically nonsense. To state the obvious: a finite area (Earth) results in a finite number of species. Applying the BD model to molecular data already shows that it does not always hold, as shown by figure 1.18.

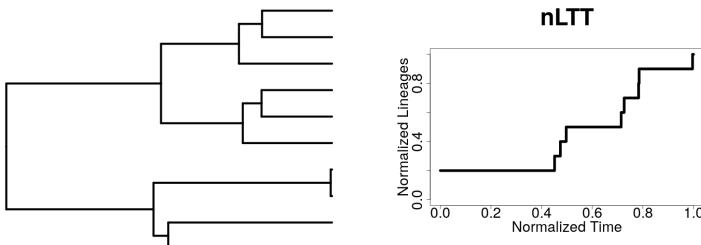


Figure 1.17 | Left: An example Birth-Death tree Right: A lineages-through-time plot of the example Birth-Death tree. In all cases, time goes from past (left) towards the present (right).

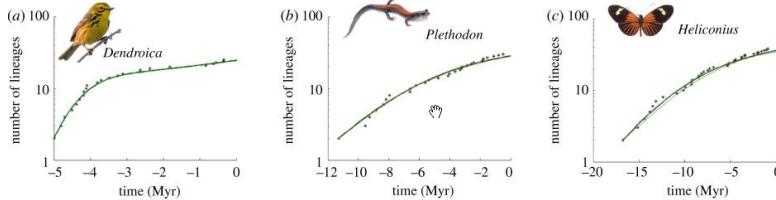


Figure 1.18 | An LTT plot for bird/lizards that shows a slowdown in speciation rate, adapted from Etienne *et al.* 2012. Because the number of lineages on the y-axis are plotted on a logarithmic scale, exponential growth would show as a straight line.

A recent study that investigates the effect of picking a wrong standard tree prior, comes from Sarver and colleagues (Sarver *et al.* 2019). In this study, they first simulate trees using either a Yule or a birth-death tree model, after which they simulate an alignment from that phylogeny using two different standard clock models. From these alignments, they inferred the original trees using all of the four different clock and tree prior combinations. They show that, regardless which priors are used, the estimated speciation and diversification rates from the inferred trees are similar to those of the original tree.

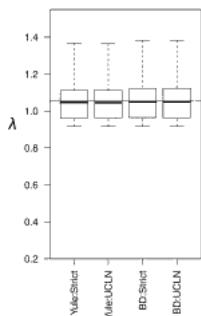


Figure 1.19 | Estimation of the speciation rate (lambda) on inferred trees using 4 evolutionary models. The original trees had 100 taxa and were simulated with a strict clock model and BD tree model, with a speciation rate of 1.104. Adapted from Sarver *et al.* 2019.

This thesis investigates the effect of picking a wrong standard tree prior, when the tree is generated by a non-standard, novel tree model. I will describe the new biological tree model that has been investigated, as well as the re-usable framework to do so.

This novel and non-standard tree model is the multiple-birth death (MBD) model [Laudanno *et al.*, 2020]. Where the standard BD models assume that a speciation event occurs in one species only at a time, the MBD models allow for speciation events to occur in multiple species at the same time. The biological idea behind this model, is that when a habitat (lake or mountain range) gets split into two, this may trigger speciation events in both communities at the same time. This mechanism is proposed as an explanation for high biodiversity in lake Tanganyika, where the water level rises and falls with ice ages, splitting up and merging the lake again and again, triggering co-occurring speciation events each change.

This thesis investigates the effect of picking a wrong standard tree prior, when the tree is generated by a non-standard tree model, using the phylogenetic software called BEAST2 (Bouckaert *et al.* 2019), an abbreviation of 'Bayesian Evolutionary Analysis by Sampling Trees'.



Figure 1.20 | BEAUti, after having picked a DNA alignment

We chose to use BEAST2 (Bouckaert *et al.* 2019) over other phylogenetic software, because BEAST2 is popular, beginner-friendly, flexible, has a package manager and a modular well-designed software architecture. The beginner-friendliness comes from the BEAST2 program called BEAUti, in which the user can set up his/her evolutionary model from a graphical user interface. There are many (in the order of dozens to hundreds) options to set up an evolutionary inference model. These choices are categorized in a site model, clock model and a tree prior.

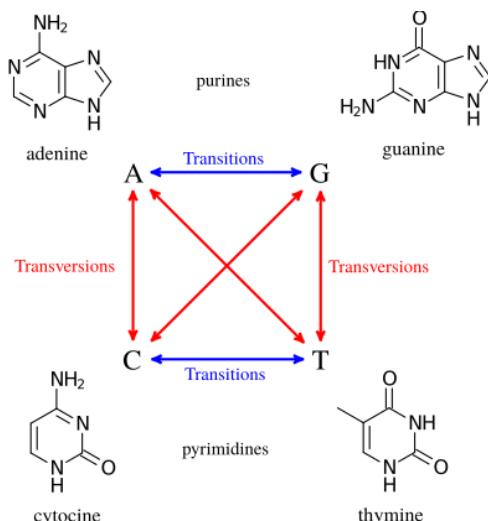


Figure 1.21 | Classification of nucleotide substitutions. The simplest nucleotide substitution model (JC69) assumes all 6 rates are equal, whereas the most complex one (GTR) allows all of these to differ.

A site model embodies the way the -in our case of DNA- nucleotides change over time. One can specify the proportion of nucleotides that changes, or let it be estimated. And how dissimilar different transition rates may be between different nucleotides. Most essential is the nucleotide substitution model, which entails the relation between the twelve transition rates from any of the four nucleotides to any of the other three nucleotides. The simplest model (called JC69) assumes all are equal, where the most complex model (called

GTR) assumes that all may differ. BEAST2 has four site models, yet there is a BEAST2 package that contains 18 additional nucleotide substitution models.

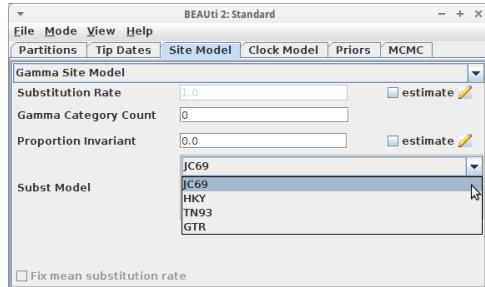


Figure 1.22 | Specifying a site model in BEAUti

To give an idea about the flexibility of BEAST2, I will zoom in on specifying one simple aspect of the inference model: the proportion invariants. The proportion invariants is the proportion, a value from zero (for 'none') to one (for 'all'), of nucleotides that remains unchanged throughout the evolutionary history. This proportion can either be set to a certain value, or be estimated. If the value is set to a certain value, BEAST2 assumes this as the truth. If the value is to be estimated by BEAST2, then one must additionally specify an initial value and a distribution how likely the different values are. By default, BEAST2 assumes a uniform distribution, that ascribes an equal probability for all values between (and including) zero to one. Instead of using a uniform distribution, there are ten other distributions that can be picked as well, allowing, for example, to assign higher probabilities to certain proportions. So, for one simple value, there is already a plethora of options, and there are even more that I will not discuss. Within BEAST2, this liberty is the rule, instead of the exception, rendering it very flexible.

The clock model embodies how the mutation rates vary between different species. The simplest clock model, called the strict clock, assumes that mutation rates are identical in all species. Two, called relaxed-clock, models assume that mutation rates between branches are independent, yet all rates are from one same distribution. The last standard clock model assumes that all species have a same mutation rate at the same time, yet these mutation rates may vary through time.



Figure 1.23 | Specifying a clock model in BEAUti

The tree prior specifies how a tree is built up, or, in our context, how speciation takes place in time, at the macro-evolutionary level. In our context, these are the Yule and Birth-Death model, which I already described earlier.



Figure 1.24 | Specifying a tree prior in BEAUti

This thesis investigates the effect of picking a wrong standard tree prior, when the tree is generated by a non-standard tree model. It does so, by using the same experimental setup, called 'pirouette', which is described in chapter 3. This framework is built up a foundation of R packages called 'babette', which is described in chapter 2.



Figure 1.25 | Environment that follows an unknown speciation model.

In the end, we want to know how well we can infer a phylogeny from molecular data found in the field. That field, outside, which follows an unknown speciation model. Let us just hope our inference is robust to whatever novel model we throw at it.

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1.1. PHOTO ATTRIBUTION

Figures 1.1, 1.2, 1.3 1.16 and 1.18 are created by scripts that can be found at https://github.com/richelbilderbeek/thesis_introduction. Figure 1.4 is taken from https://commons.wikimedia.org/wiki/File:Darwin_Tree_1837.png. The drawing of Darwin's finches in figure 1.5 is taken from https://commons.wikimedia.org/wiki/File:Darwin%27s_finches_by_Gould.jpg. The evolution of Homoniniae in figure 1.6 is made by Dbachmann and taken from https://en.wikipedia.org/wiki/File:Hominini_lineage.svg. The phylogeny of figure 1.9 is by Aglondon, from https://commons.wikimedia.org/wiki/File:Edge_tree.png. The Largetooth Sawfish of figure 1.9 is taken from <http://www.edgeofexistence.org/species/largetooth-sawfish>. Figure 1.10 is taken from the PHYLIP homepage at <http://evolution.genetics.washington.edu/phylip.html>. The BEAST2 logo within figure ??, as well as the DensiTree picture are taken from the BEAST2 homepage at <http://www.beast2.org>. Figures 1.20, 1.22, 1.23, and 1.24 are actual screenshots from BEAUTi v2.6.1. Figure 1.21 is from https://commons.wikimedia.org/wiki/File:Transitions_and_transversions.svg. The image of figure 1.25 is from https://commons.wikimedia.org/wiki/File:The_Earth_seen_from_Apollo_17.jpg.