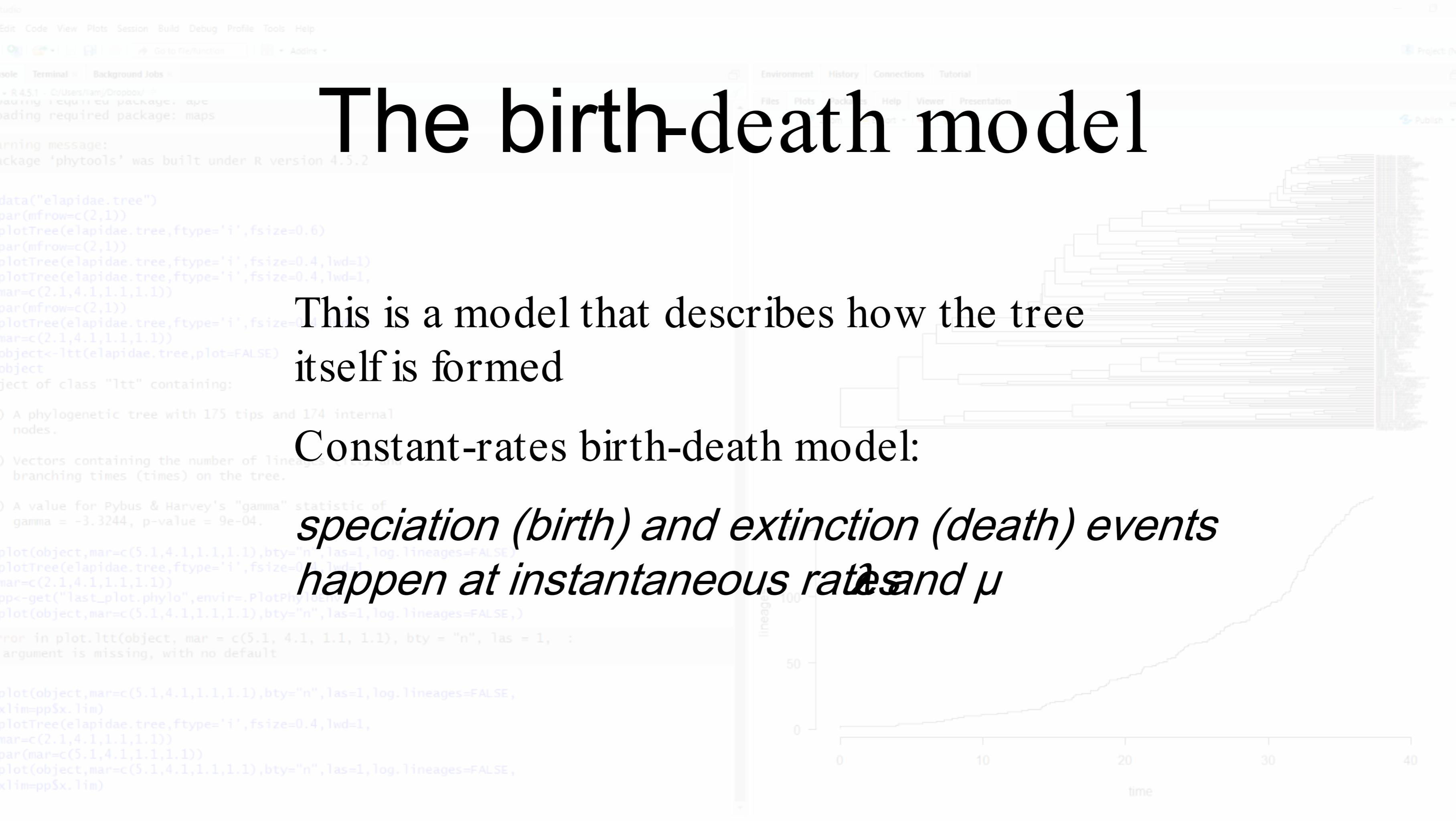


# Introduction to diversification

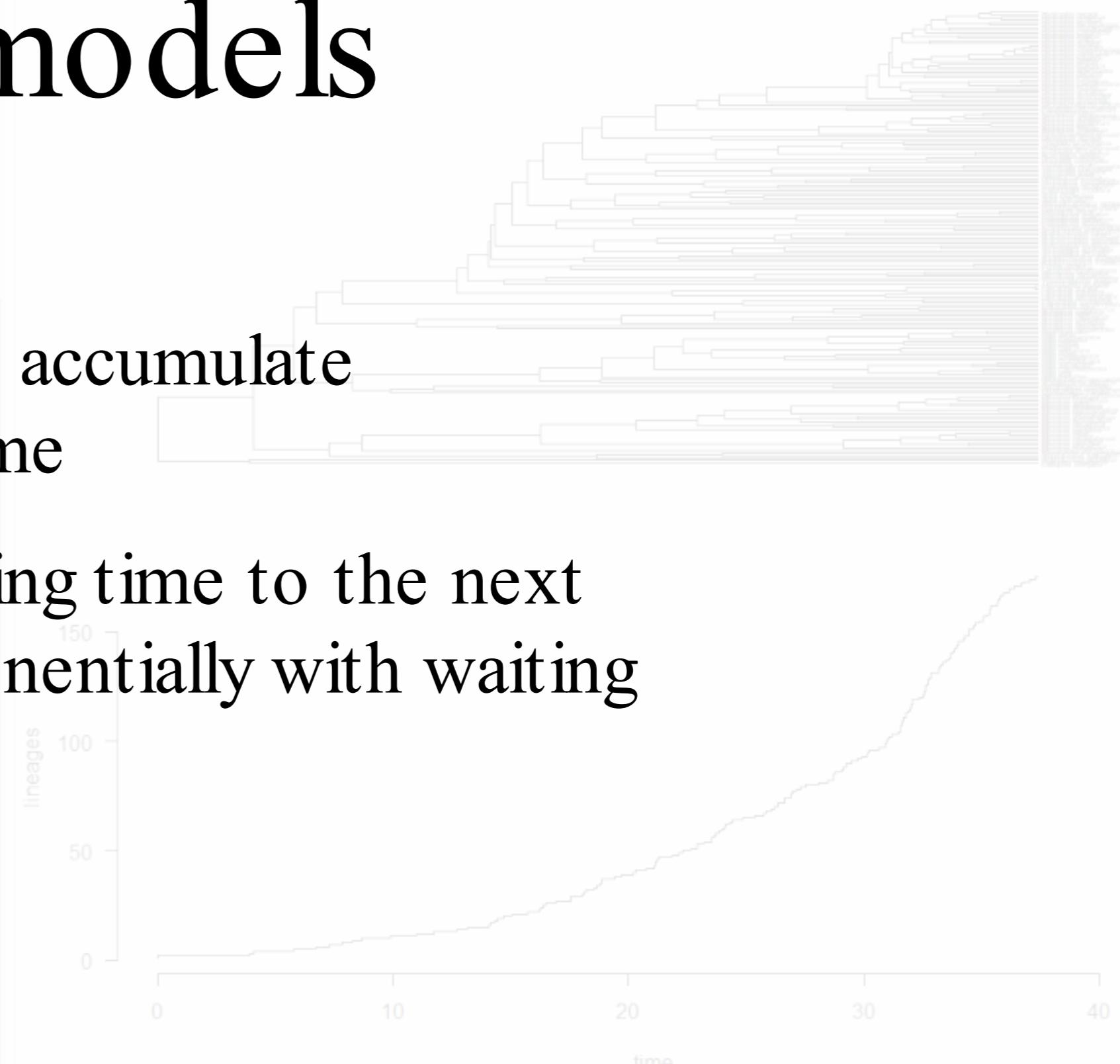


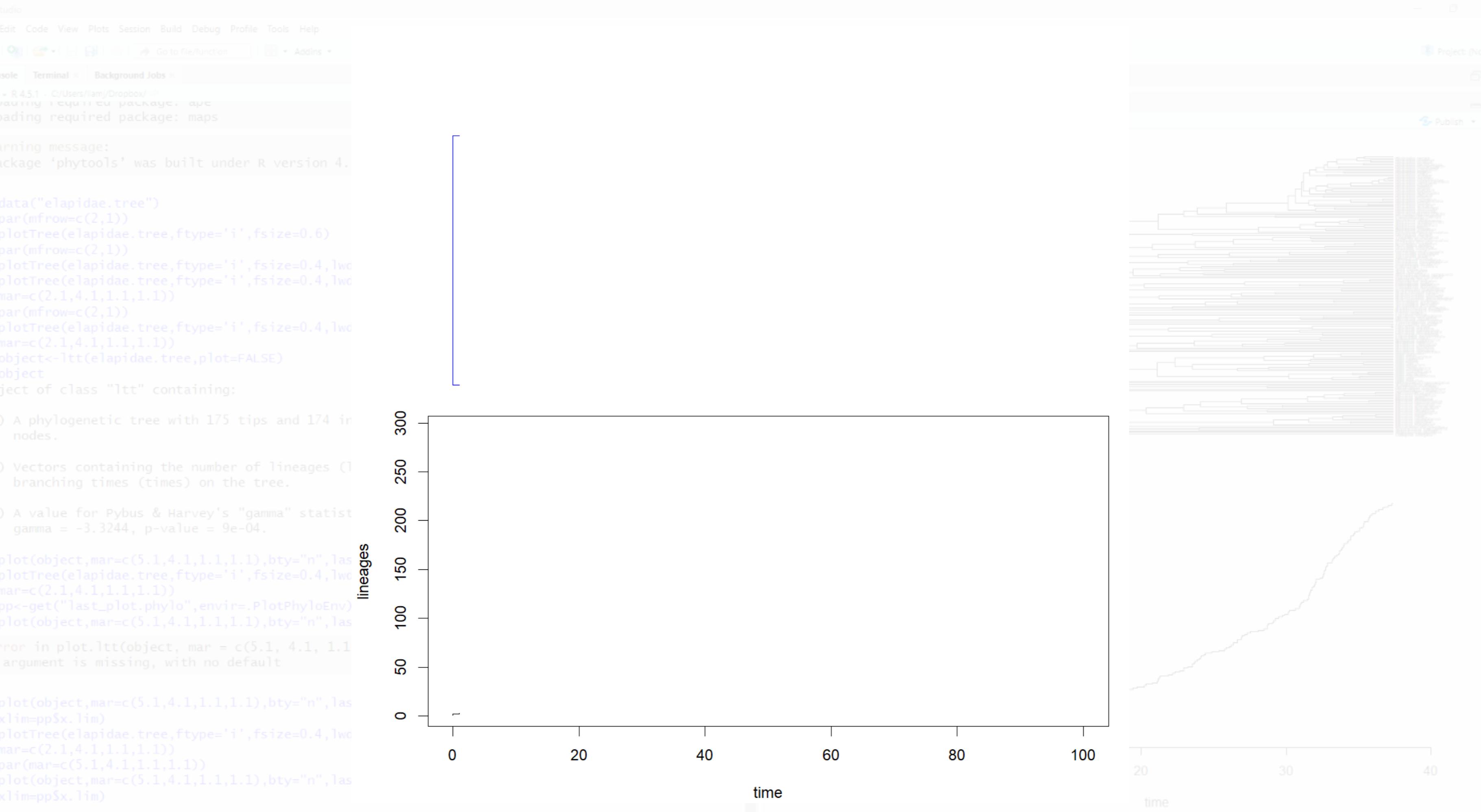


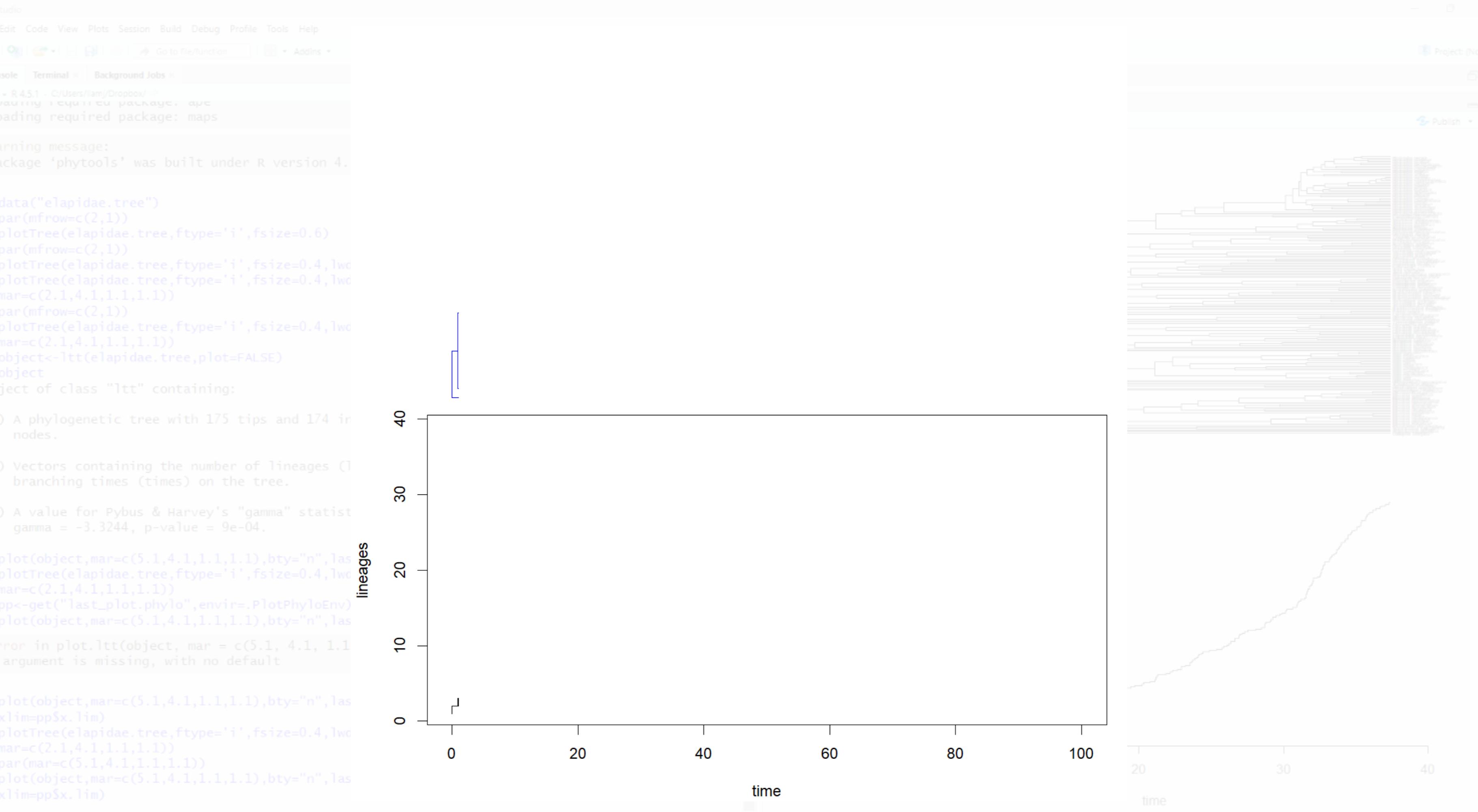
# Properties of birth-death models

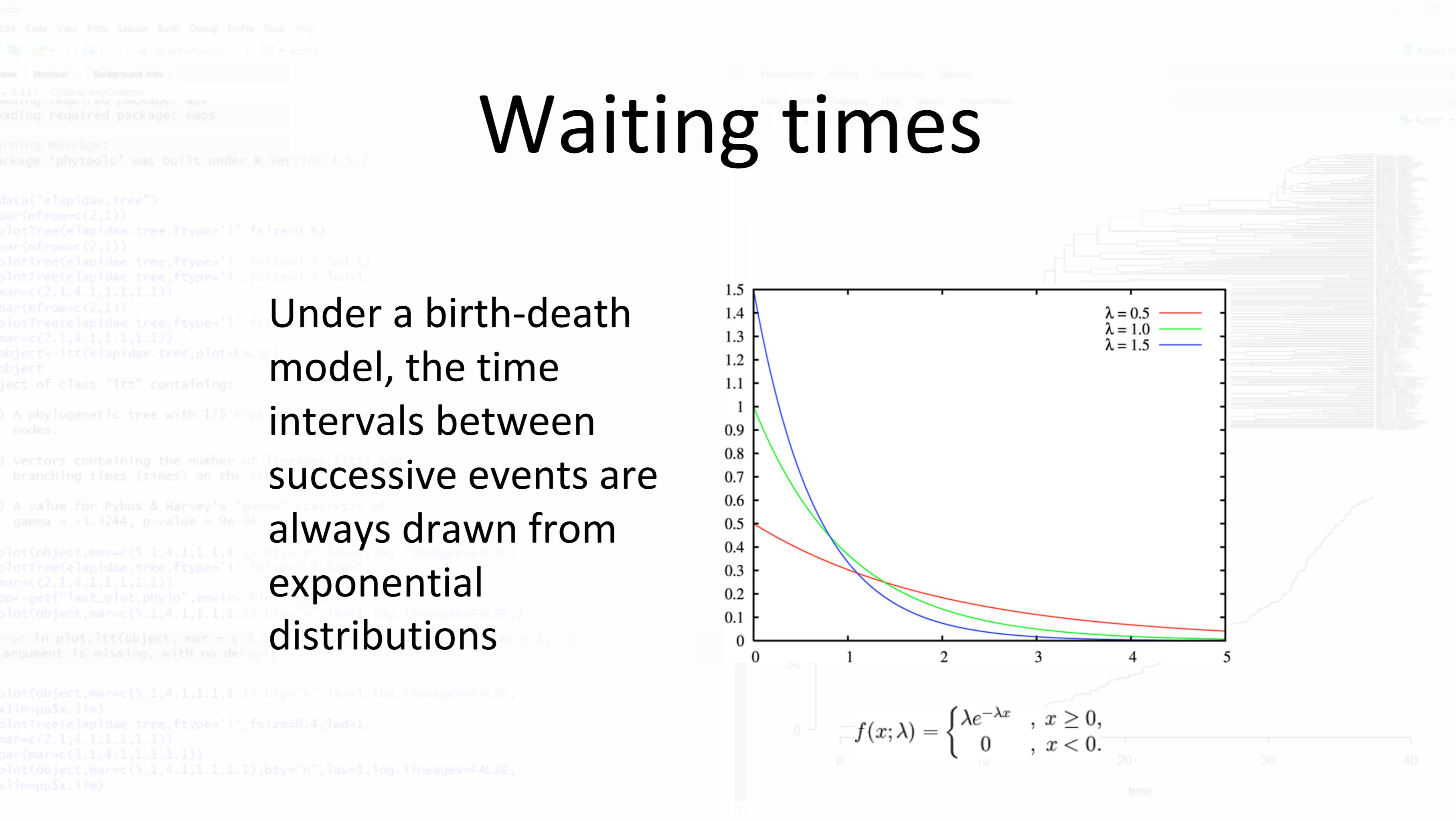
As long as  $\lambda > \mu$  lineages accumulate exponentially through time

For any lineage, the waiting time to the next event is distributed exponentially with waiting time  $\lambda + \mu$









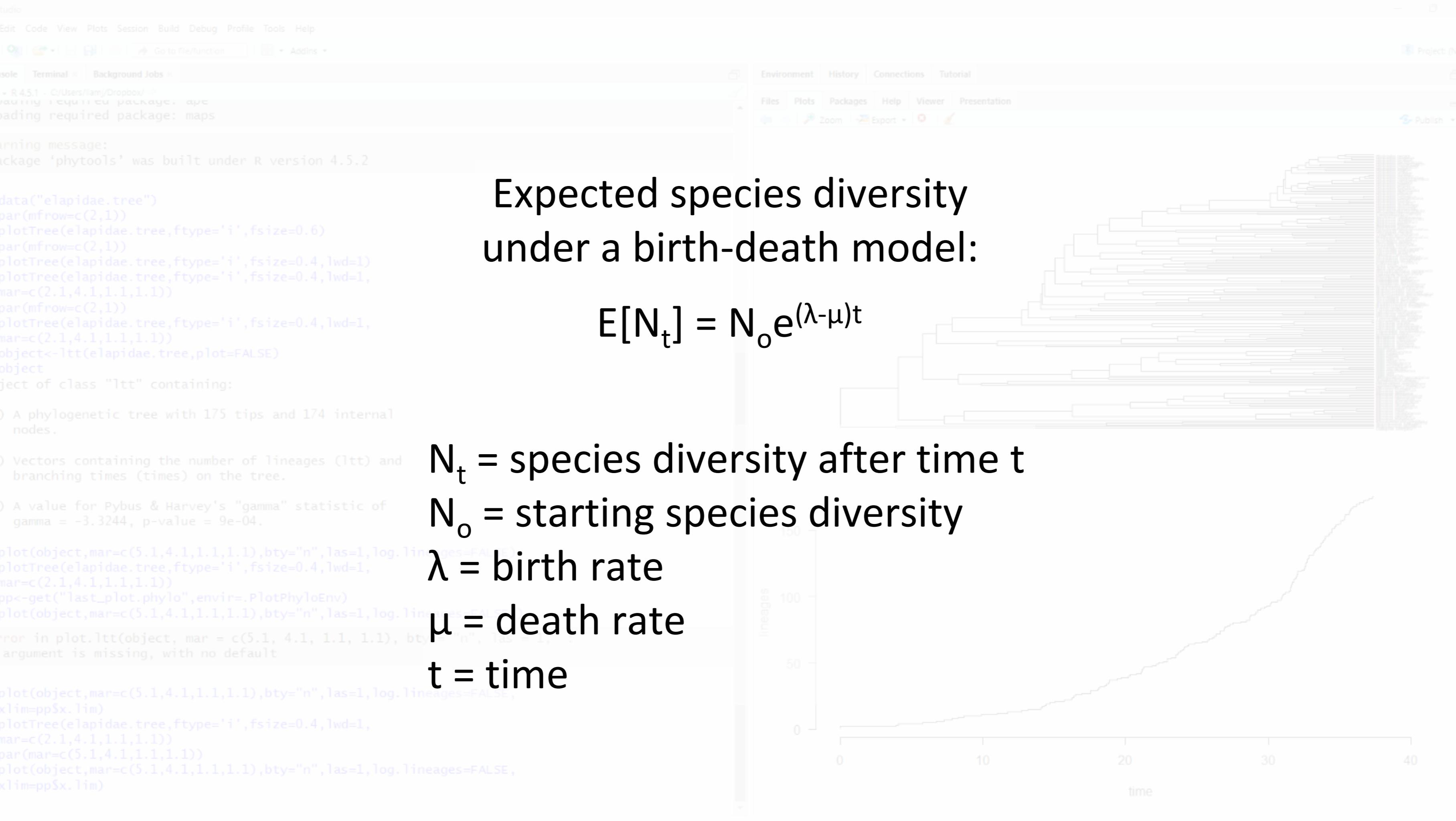
```
Edit Code View Plots Session Build Debug Profile Tools Help
File Go To Function Addins
Console Terminal Background Jobs
R 4.5.1 - C:/Users/lamj/Dropbox/
  warning: required package: ape
  loading required package: maps
  warning message:
  package 'phytools' was built under R version 4.5.2

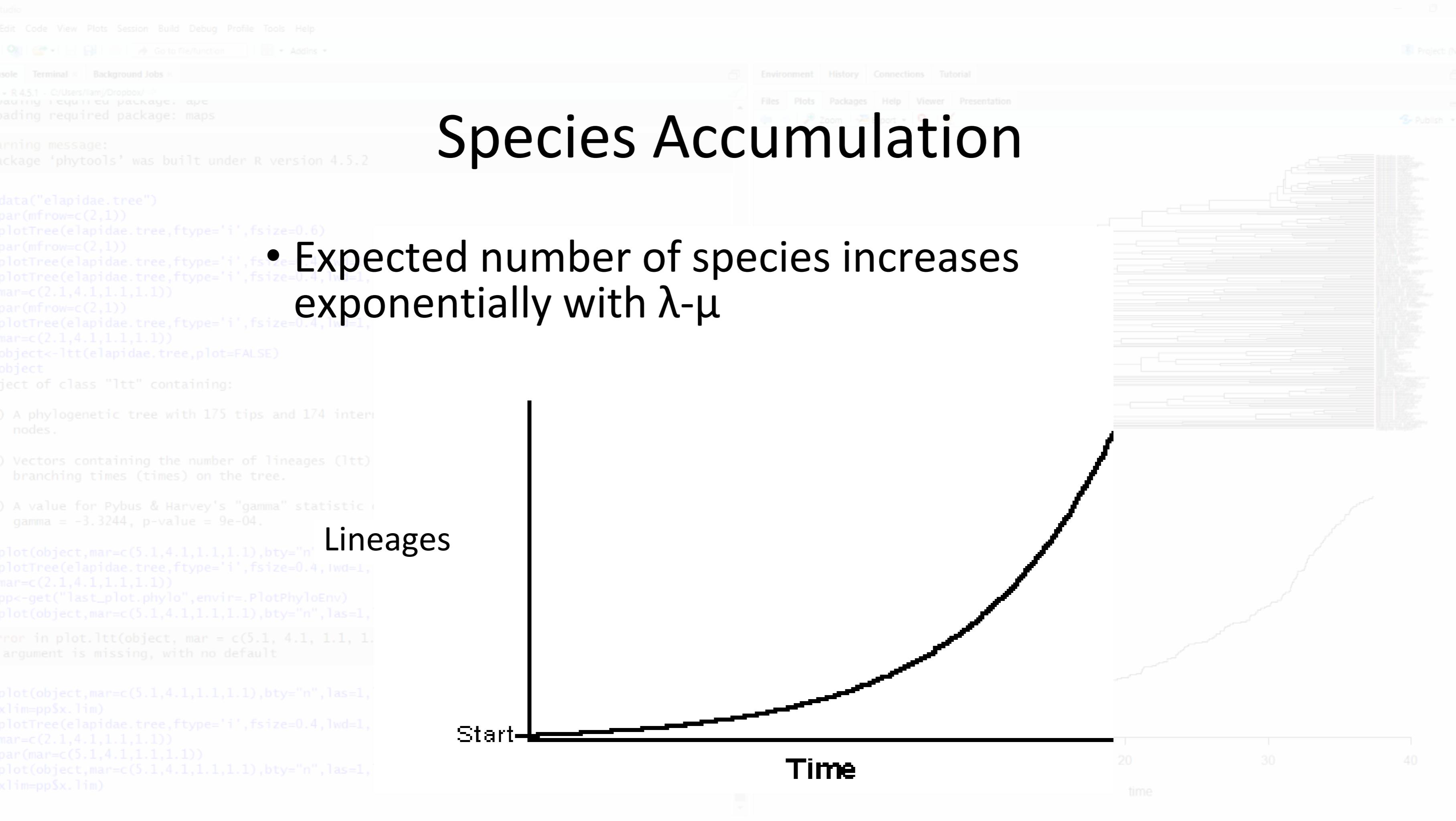
data("elapidae.tree")
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fsize=0.6)
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1)
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1,
        mar=c(2.1,4.1,1.1,1.1))
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1)
mar=c(2.1,4.1,1.1,1.1))
object<-ltt(elapidae.tree,plot=FALSE)
object
object of class "ltt" containing:
  A phylogenetic tree with 175 tips and 174 internal nodes.
  Vectors containing the number of lineages (ltt) and branching times (times) on the tree.
  A value for Pybus & Harvey's "gamma" statistic of gamma = -3.3244, p-value = 9e-04.

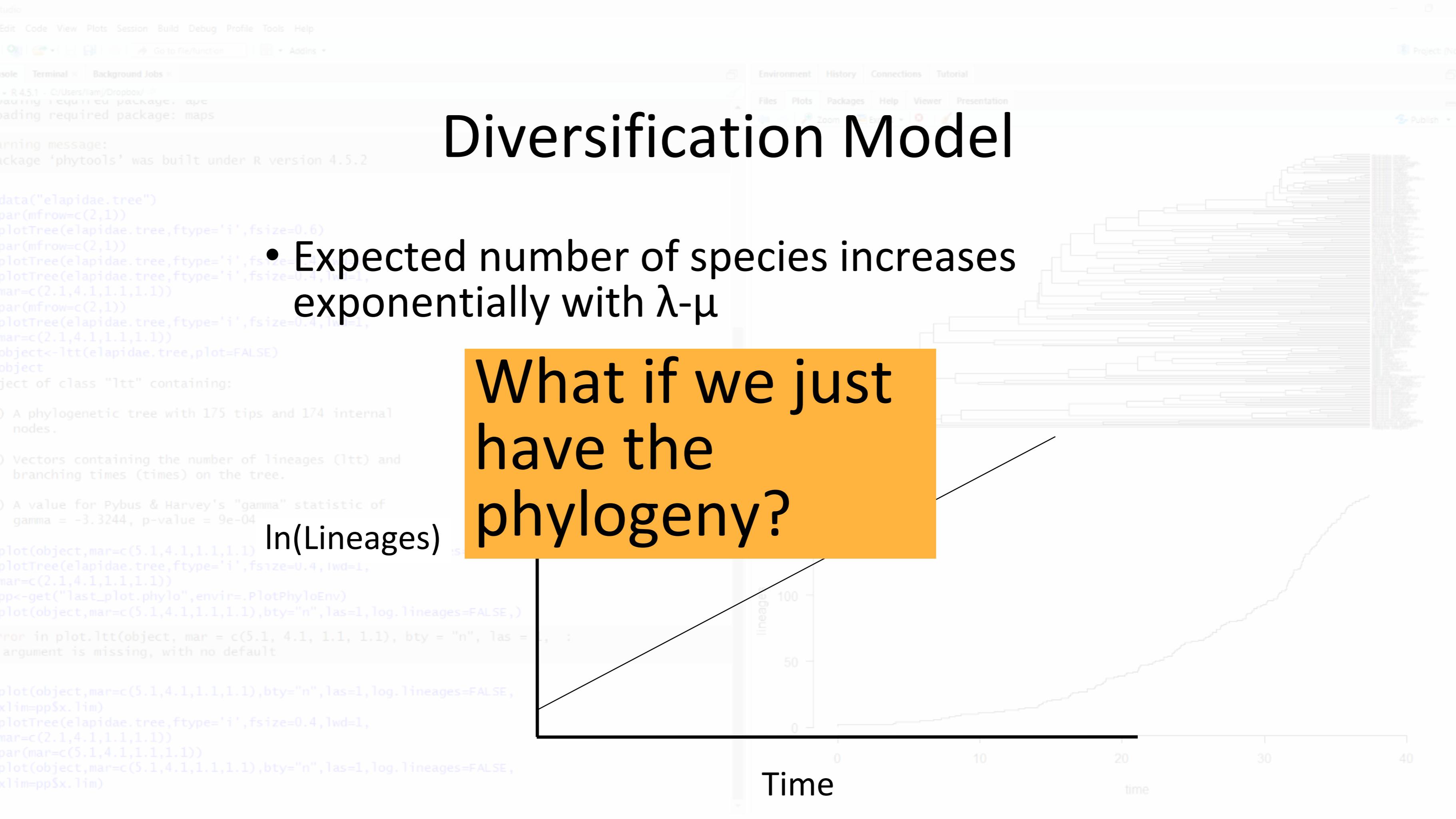
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE)
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1,
        mar=c(2.1,4.1,1.1,1.1))
op<-get("last_plot.phylo",envir=.PlotEnv)
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE,)

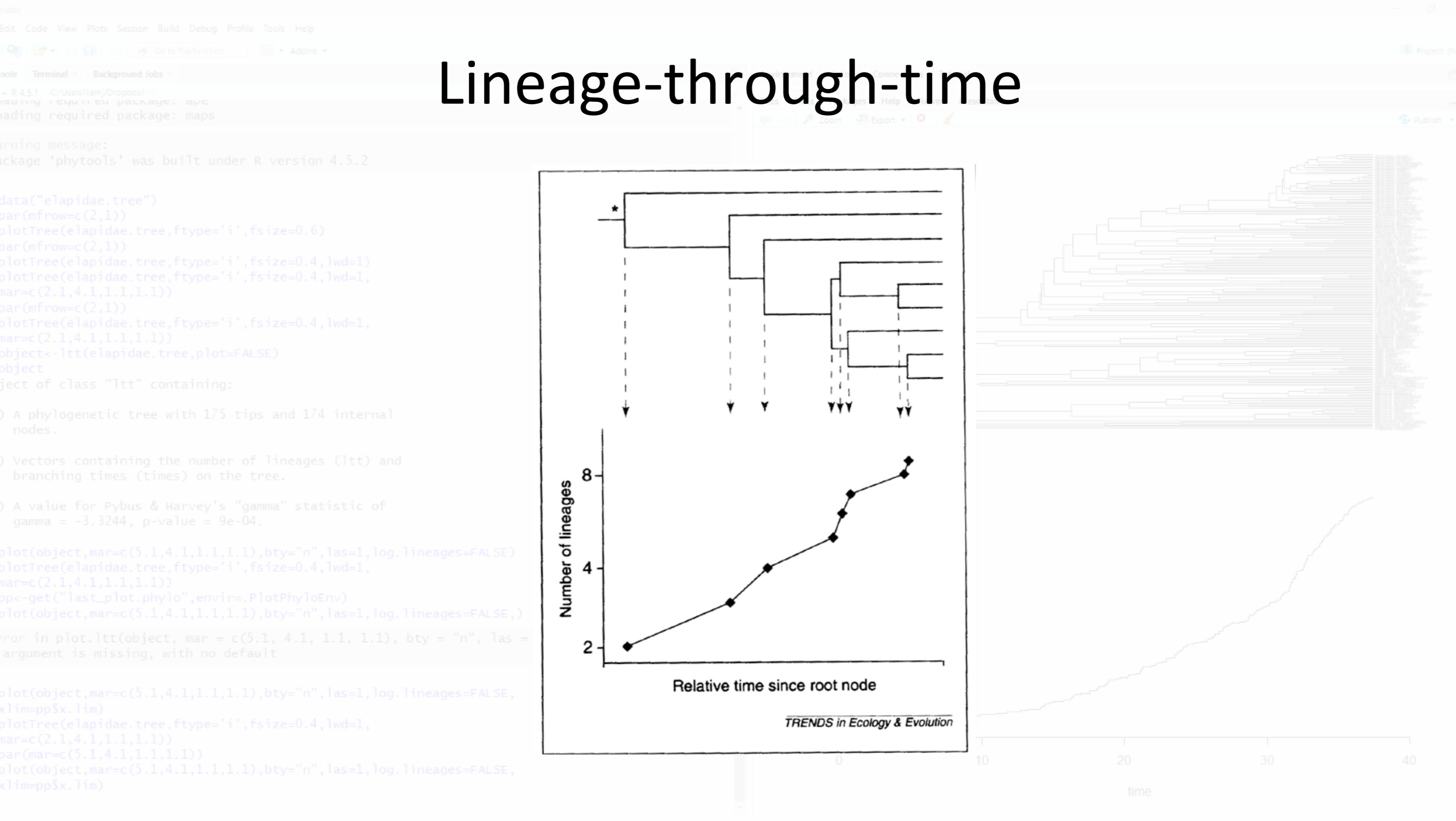
error in plot.ltt(object, mar = c(5.1, 4.1, 1.1, 1.1)) : argument is missing, with no default

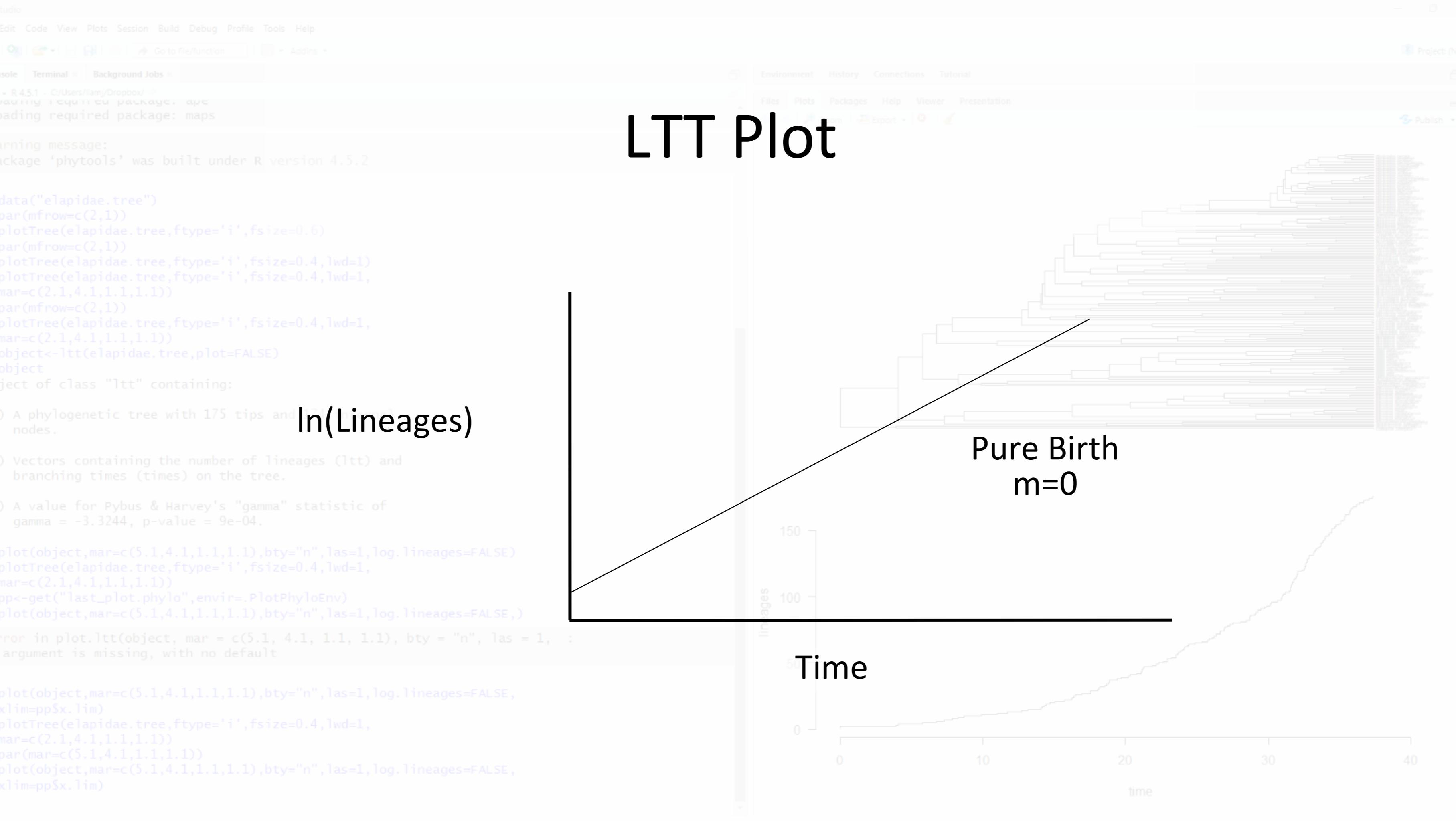
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE,
      xlim=pp$X.lim)
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1,
        mar=c(2.1,4.1,1.1,1.1))
par(mar=c(5.1,4.1,1.1,1.1))
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE,
      xlim=pp$X.lim)
```

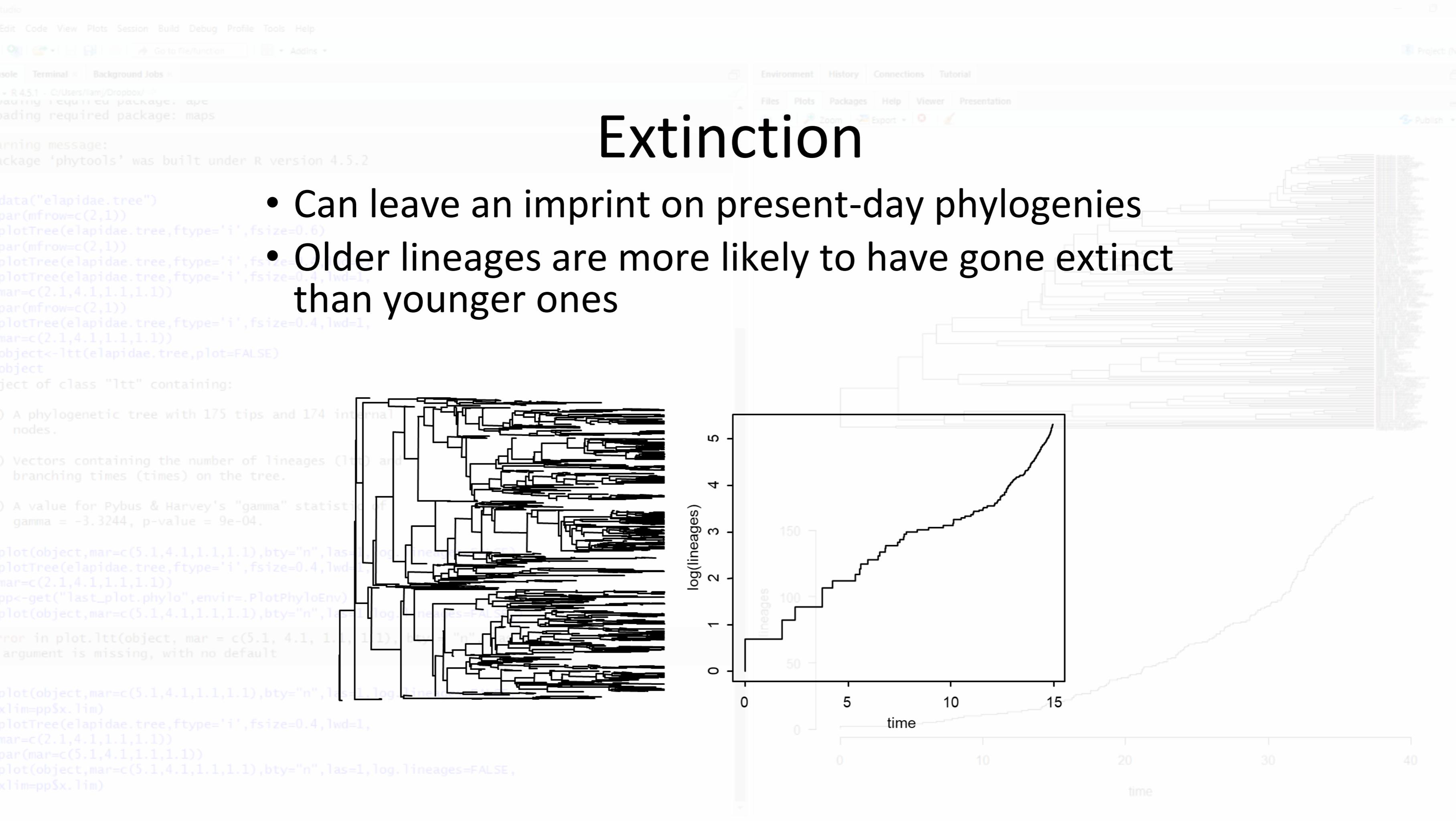


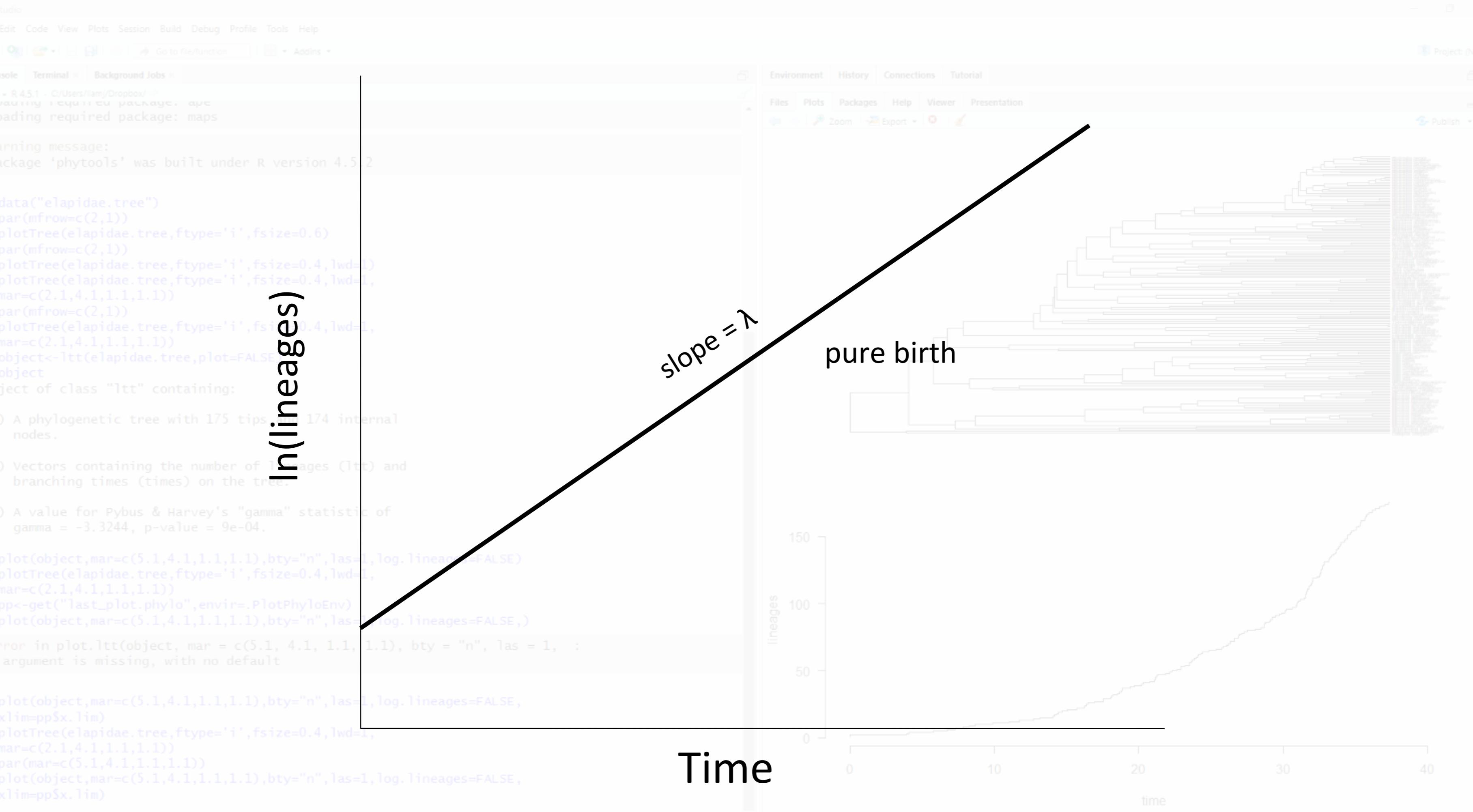


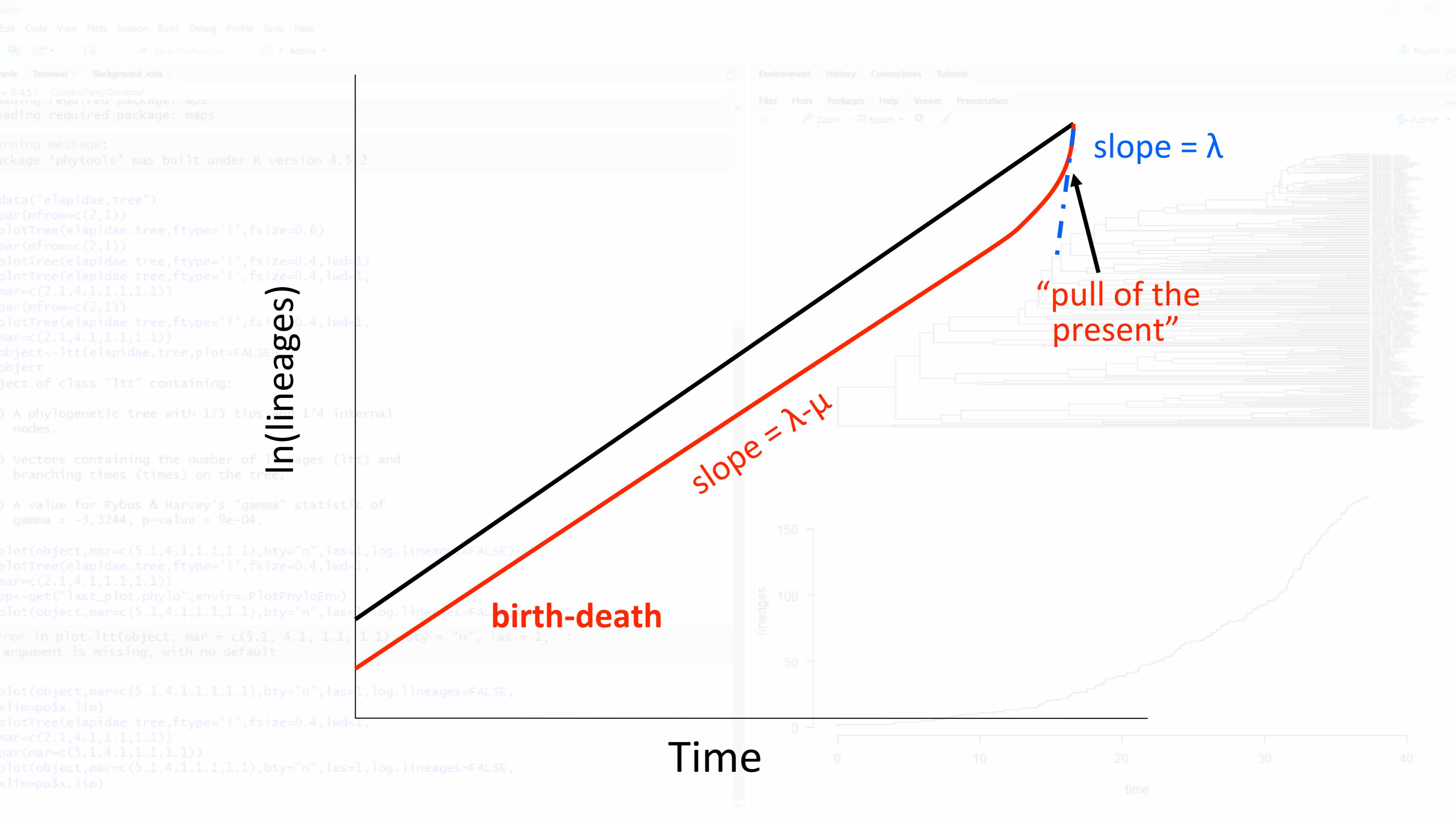


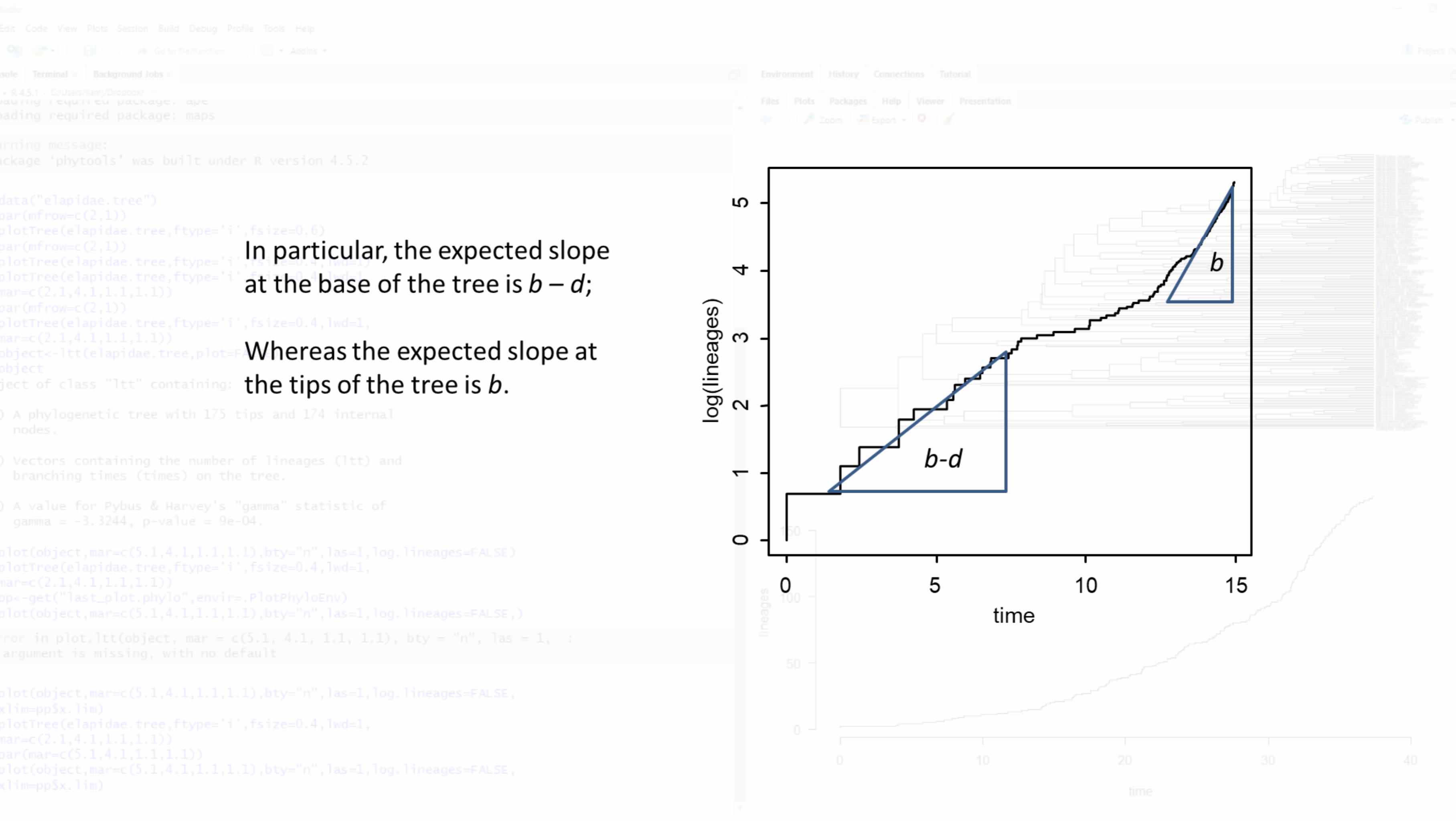












In particular, the expected slope at the base of the tree is  $b - d$ ;

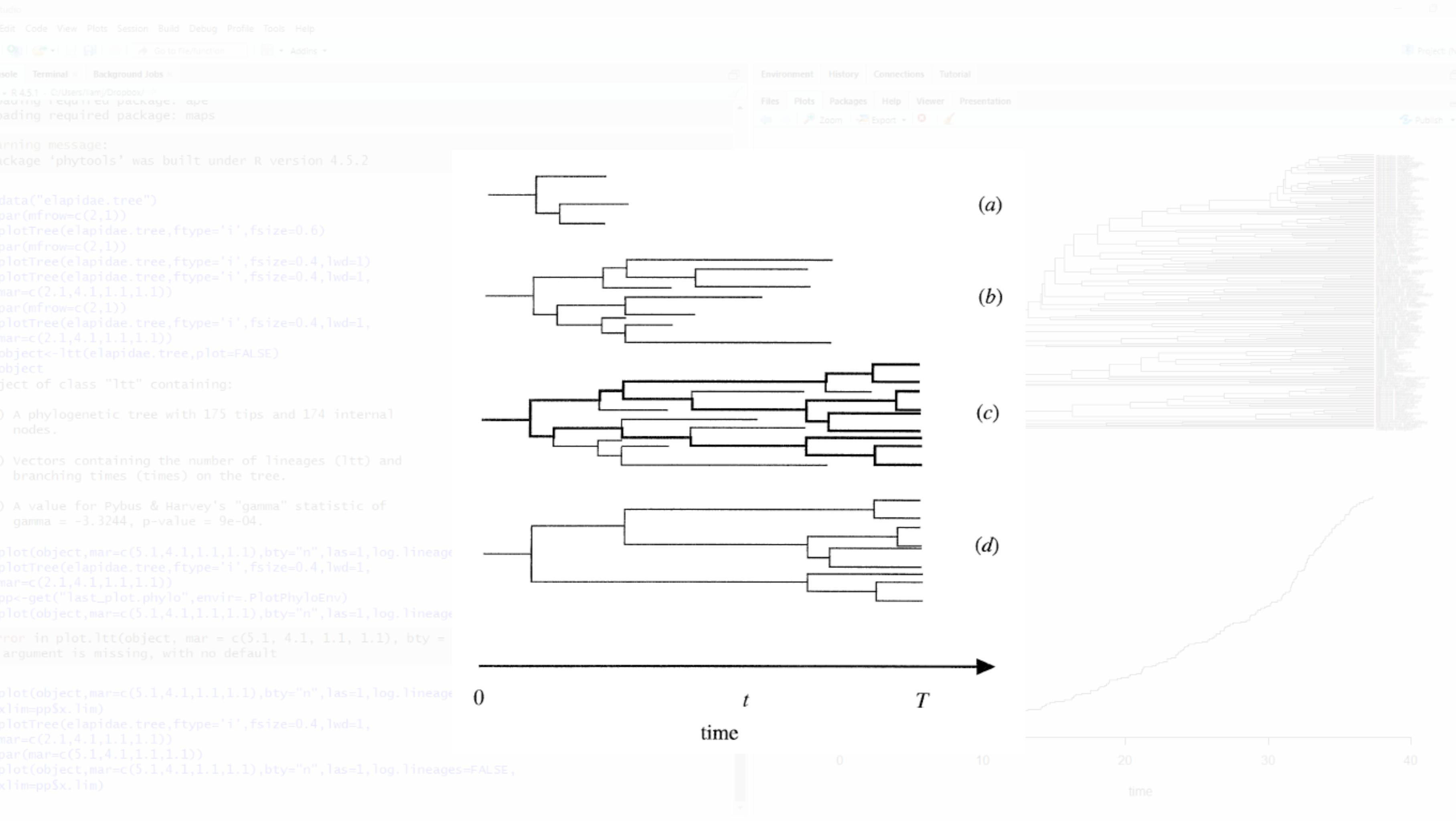
Whereas the expected slope at the tips of the tree is  $b$ .

```
data("elapidae.tree")
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fsiz=0.6)
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fsiz=0.4,lwd=1)
plotTree(elapidae.tree,ftype='i',fsiz=0.4,lwd=1,
mar=c(2.1,4.1,1.1,1.1))
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fsiz=0.4,lwd=1,
mar=c(2.1,4.1,1.1,1.1))
object<-ltt(elapidae.tree,plot=FALSE)
object
object of class "ltt" containing:
  A phylogenetic tree with 175 tips and 174 internal nodes.
  Vectors containing the number of lineages (ltt) and branching times (times) on the tree.
  A value for Pybus & Harvey's "gamma" statistic of gamma = -3.3244, p-value = 9e-04.

plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE)
plotTree(elapidae.tree,ftype='i',fsiz=0.4,lwd=1,
mar=c(2.1,4.1,1.1,1.1))
op<-get("last_plot.phylo",envir=.PlotPhyloEnv)
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE,)

error in plot.ltt(object, mar = c(5.1, 4.1, 1.1, 1.1), bty = "n", las = 1, :
  argument is missing, with no default

plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE,
xlim=pp$xF)
plotTree(elapidae.tree,ftype='i',fsiz=0.4,lwd=1,
mar=c(2.1,4.1,1.1,1.1))
par(mar=c(5.1,4.1,1.1,1.1))
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE,
xlim=pp$xF)
```



```
data("elapidae.tree")
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fsize=
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fsize=
plotTree(elapidae.tree,ftype='i',fsize=
mar=c(2.1,4.1,1.1,1.1))
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fsize=
mar=c(2.1,4.1,1.1,1.1))
object<-ltt(elapidae.tree,plot=FALSE)
object
```

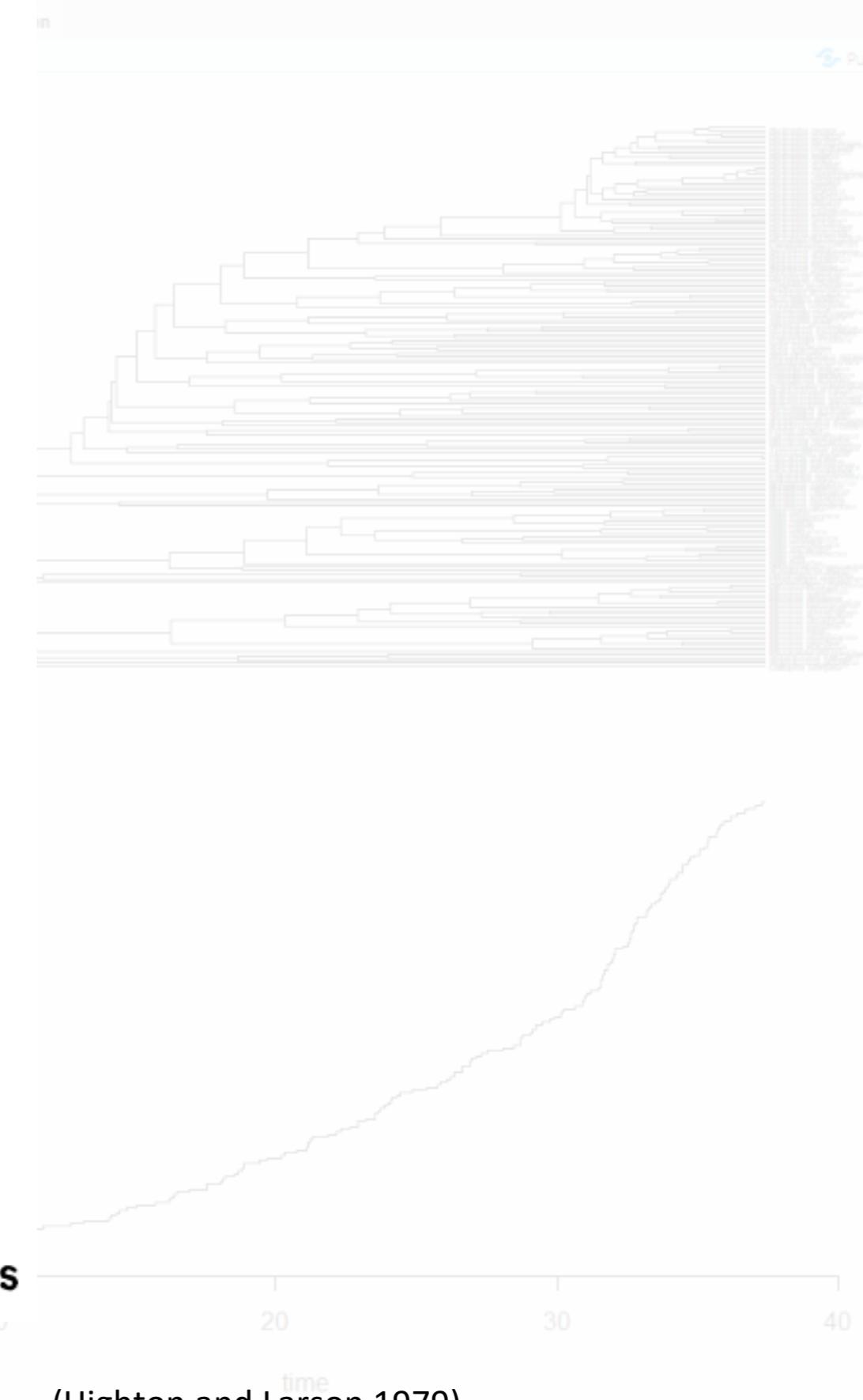
Object of class "ltt" containing:

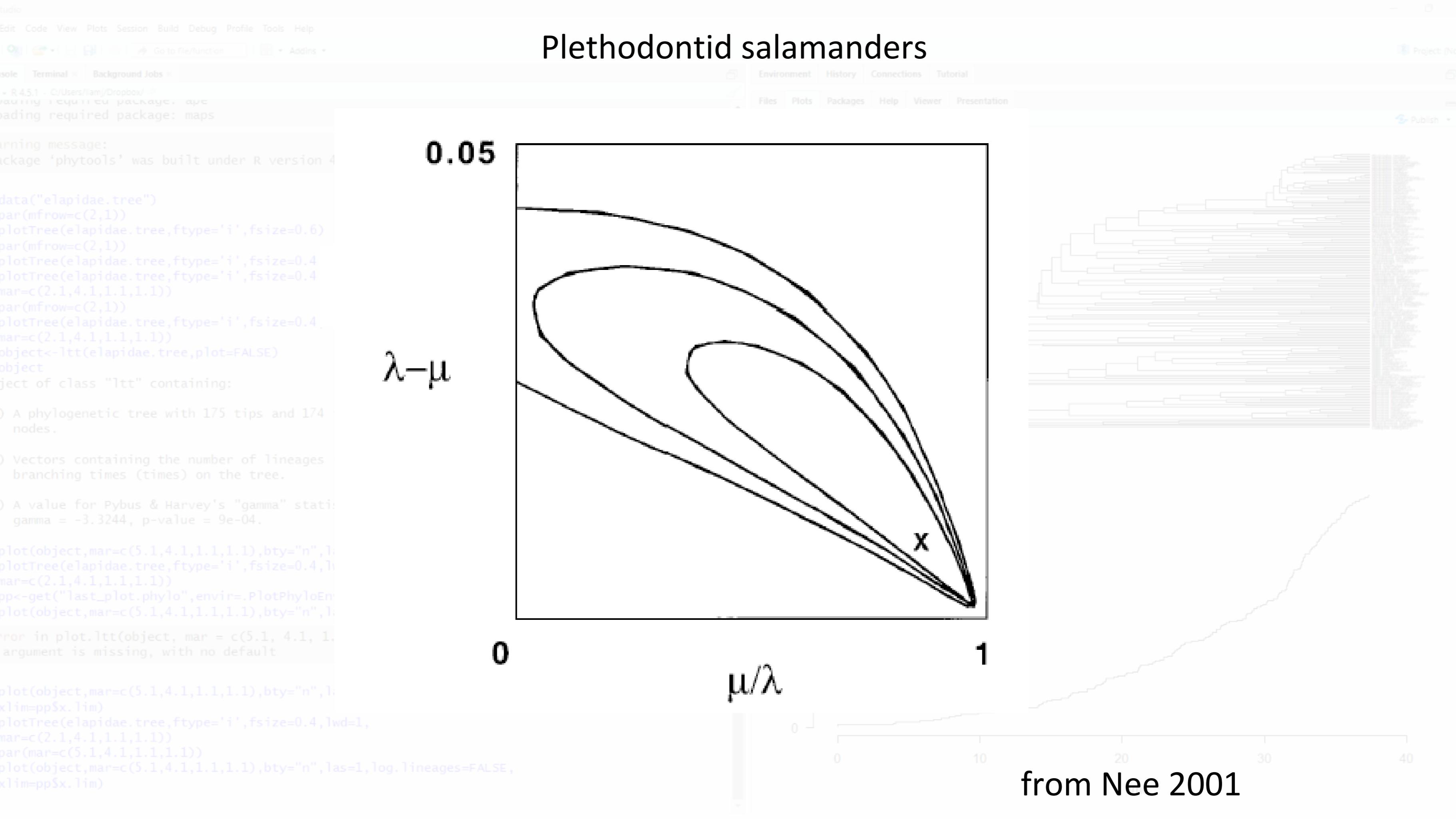
- ) A phylogenetic tree with 175 tips and nodes.
- ) Vectors containing the number of line branching times (times) on the tree.
- ) A value for Pybus & Harvey's "gamma"  
gamma = -3.3244, p-value = 9e-04.

```
plot(object,mar=c(5.1,4.1,1.1,1.1),bty=
plotTree(elapidae.tree,ftype='i',fsize=
mar=c(2.1,4.1,1.1,1.1))
op<-get("last_plot.phylo",envir=.PlotPhy)
plot(object,mar=c(5.1,4.1,1.1,1.1),bty=
error in plot.ltt(object, mar = c(5.1, 4
argument is missing, with no default
```

```
plot(object,mar=c(5.1,4.1,1.1,1.1),bty=
xlim=pp$xFlim)
plotTree(elapidae.tree,ftype='i',fsize=
mar=c(2.1,4.1,1.1,1.1))
par(mar=c(5.1,4.1,1.1,1.1))
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE,
xlim=pp$xFlim)
```

# Plethodontid salamanders





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Edit Code View Plots Session Build Debug Profile Tools Help

File Addins

Console Terminal Background Jobs

R 4.5.1 - C:/Users/lamj/Dropbox/  
loading required package: maps

Warning message:

package 'phytools' was built under R version 4

data("elapidae.tree")  
par(mfrow=c(2,1))  
plotTree(elapidae.tree,ftype='i',fsize=0.6)  
par(mfrow=c(2,1))  
plotTree(elapidae.tree,ftype='i',fsize=0.4)  
plotTree(elapidae.tree,ftype='i',fsize=0.4  
mar=c(2.1,4.1,1.1,1.1))  
par(mfrow=c(2,1))  
plotTree(elapidae.tree,ftype='i',fsize=0.4,  
mar=c(2.1,4.1,1.1,1.1))  
object<-ltt(elapidae.tree,plot=FALSE)object of class "ltt" containing:  
A phylogenetic tree with 175 tips and 174 nodes.

Vectors containing the number of lineages branching times (times) on the tree.

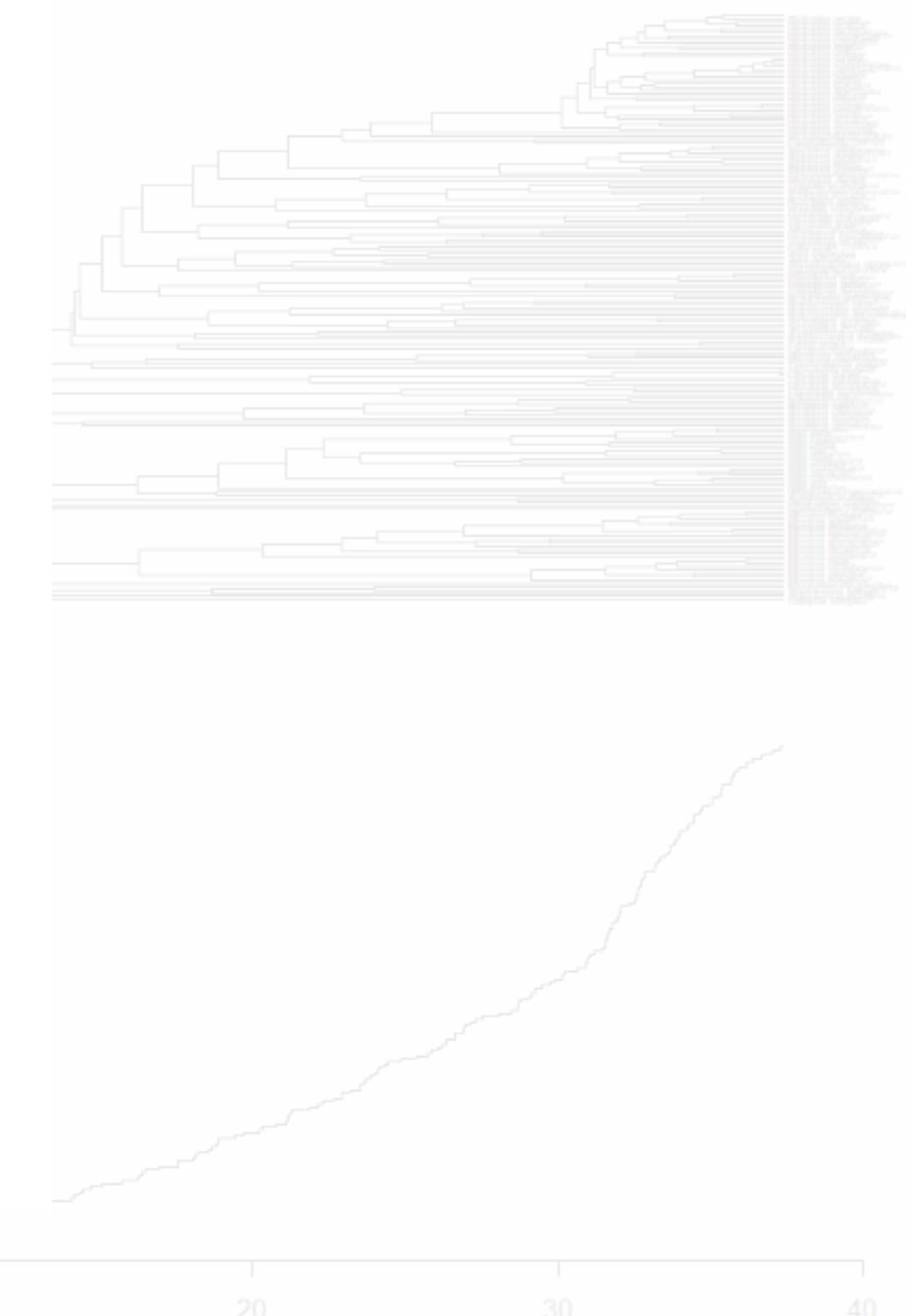
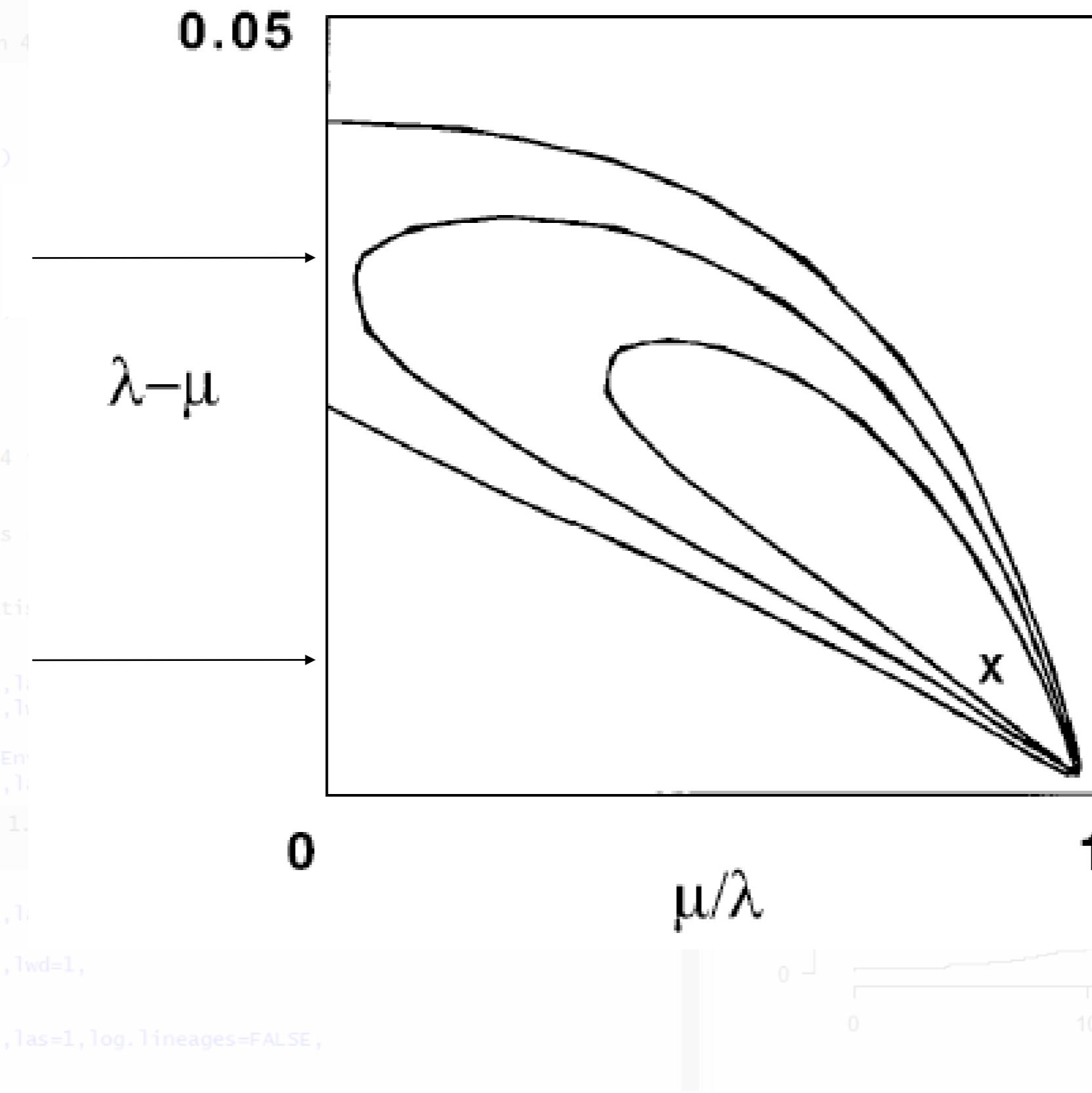
A value for Pybus & Harvey's "gamma" statistic:  
gamma = -3.3244, p-value = 9e-04.plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",l  
plotTree(elapidae.tree,ftype='i',fsize=0.4,l  
mar=c(2.1,4.1,1.1,1.1))  
op<-get("last\_plot.phylo",envir=.PlotPhyloEnv)  
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",l  
rror in plot.ltt(object, mar = c(5.1, 4.1, 1.  
argument is missing, with no defaultplot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",l  
xlim=pp\$xFlim)  
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1,  
mar=c(2.1,4.1,1.1,1.1))  
par(mar=c(5.1,4.1,1.1,1.1))  
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE,  
xlim=pp\$xFlim)

# Plethodontid salamanders

Environment History Connections Tutorial

Files Plots Packages Help Viewer Presentation

Project [None]



```
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Edit Code View Plots Session Build Debug Profile Tools Help
File Go to File/Function Addins
Console Terminal Background Jobs
R 4.5.1 - C:/Users/lamj/Dropbox/
Warning: required package: ape
Loading required package: maps
Warning message:
package 'phytools' was built under R version 4.5.2

data("elapidae.tree")
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fsize=0.6)
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1)
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1,
mar=c(2.1,4.1,1.1,1.1))
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1,
mar=c(2.1,4.1,1.1,1.1))
object<-ltt(elapidae.tree,plot=FALSE)
object
object of class "ltt" containing:
A phylogenetic tree with 175 tips and 174 internal nodes.
Vectors containing the number of lineages (ltt) and branching times (times) on the tree.
A value for Pybus & Harvey's "gamma" statistic of gamma = -3.3244, p-value = 9e-04.

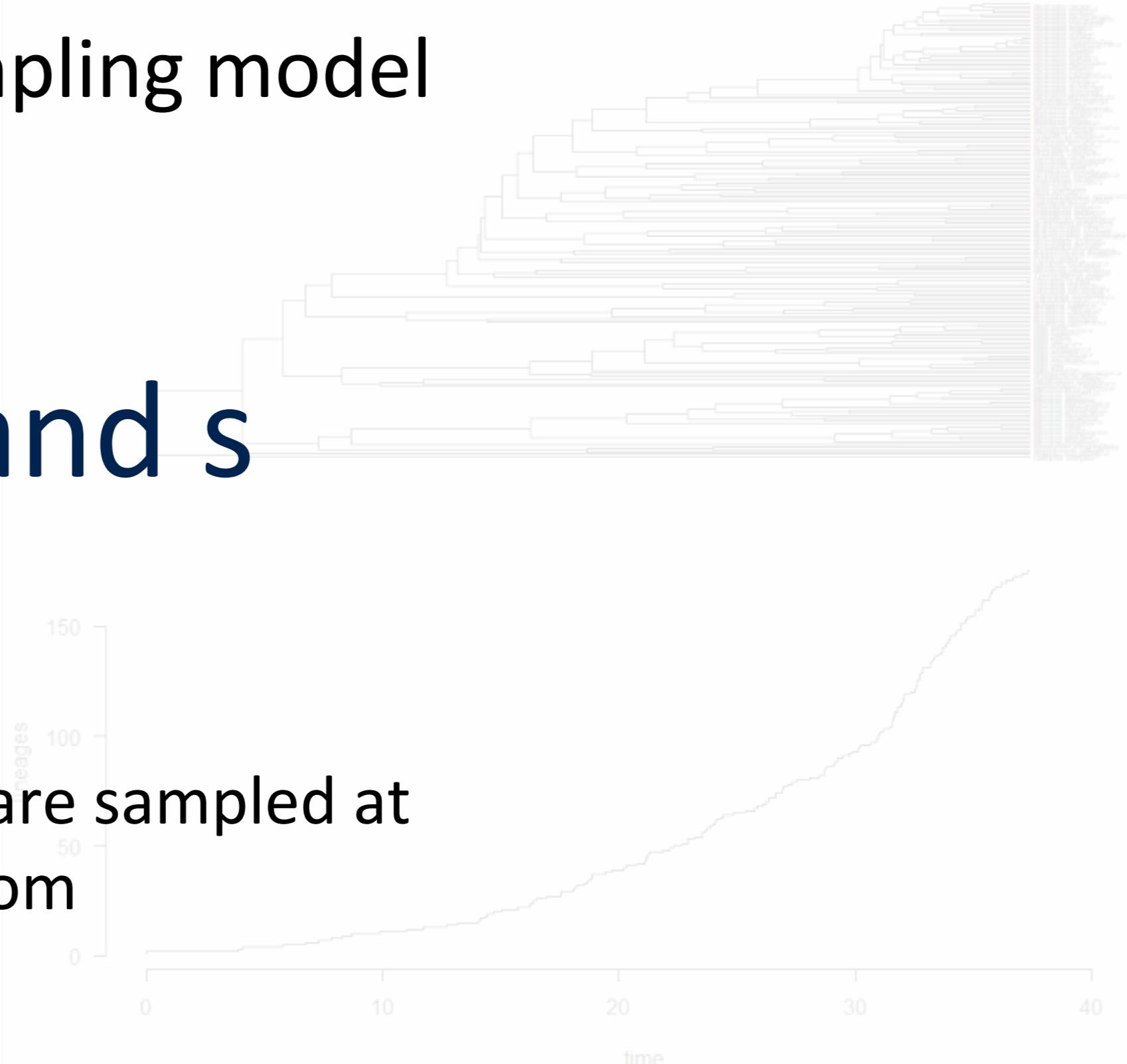
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE)
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1,
mar=c(2.1,4.1,1.1,1.1))
op<-get("last_plot.phylo",envir=.PlotPhyloEnv)
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE,)
Error in plot.ltt(object, mar = c(5.1, 4.1, 1.1, 1.1), bty = " argument is missing, with no default

plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE,
xlim=pp$xFlim)
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1,
mar=c(2.1,4.1,1.1,1.1))
par(mar=c(5.1,4.1,1.1,1.1))
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE,
xlim=pp$xFlim)
```

# Birth-death-sampling model

$\lambda$ ,  $\mu$ , and  $s$

Assume species are sampled at random



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| Go to File/Function Addins Project Node

Console Terminal > Background Jobs >

R 4.5.1 - C:/Users/lamj/Dropbox/...  
Warning: required package: ape  
loading required package: maps

Warning message:  
package 'phytools' was built under R version 4.5.2

```
data("elapidae.tree")
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fsize=0.6)
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1)
plotTree
mar=c(2
par(mfr
plotTre
mar=c(2
object<
object
ject of
) A phy
nodes
) Vecto
branc
) A value for Pybus & Harvey's "gamma" statistic of
gamma = -3.3244, p-value = 9e-04.
```

Syst Biol. 2012 Oct;61(5):785-92. doi: 10.1093/sysbio/sys031. Epub 2012 Feb 14.

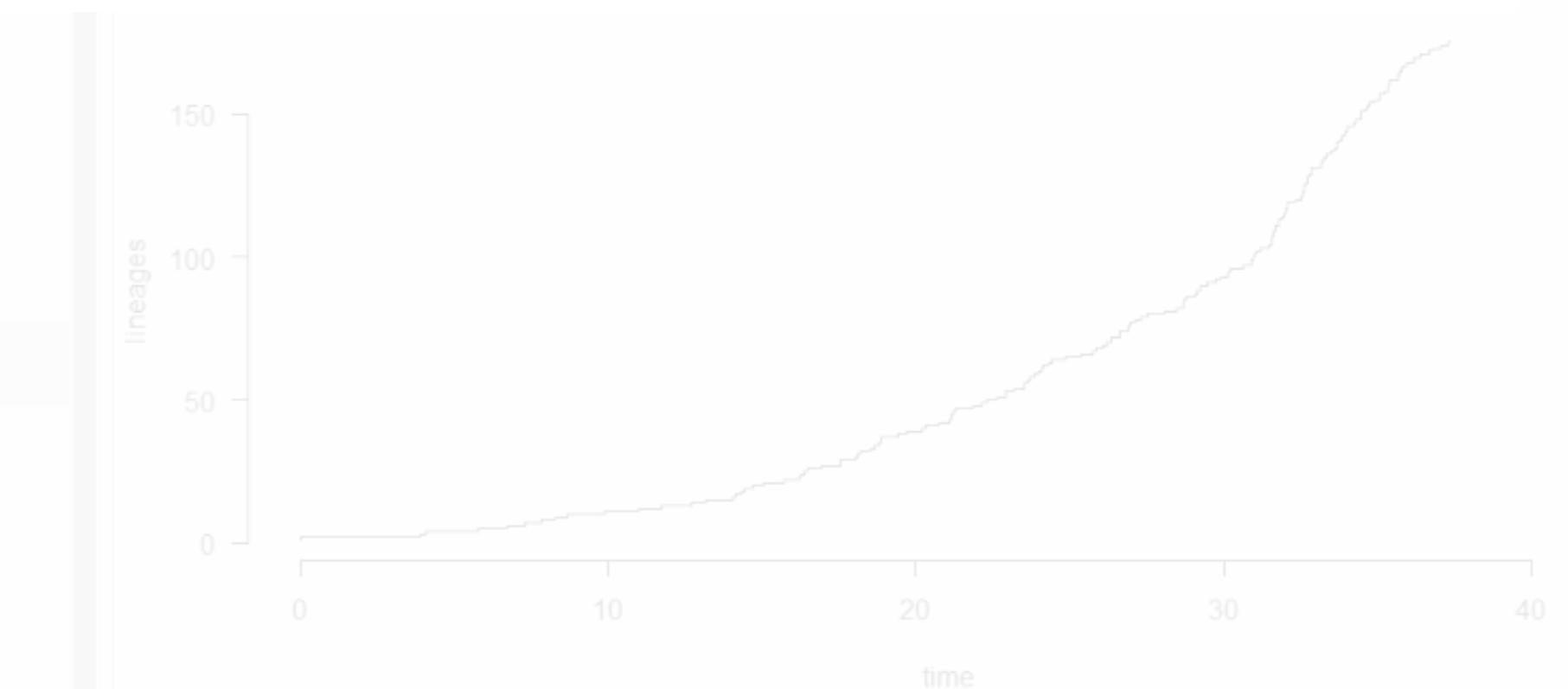
## A new method for handling missing species in diversification analysis applicable to randomly or nonrandomly sampled phylogenies.

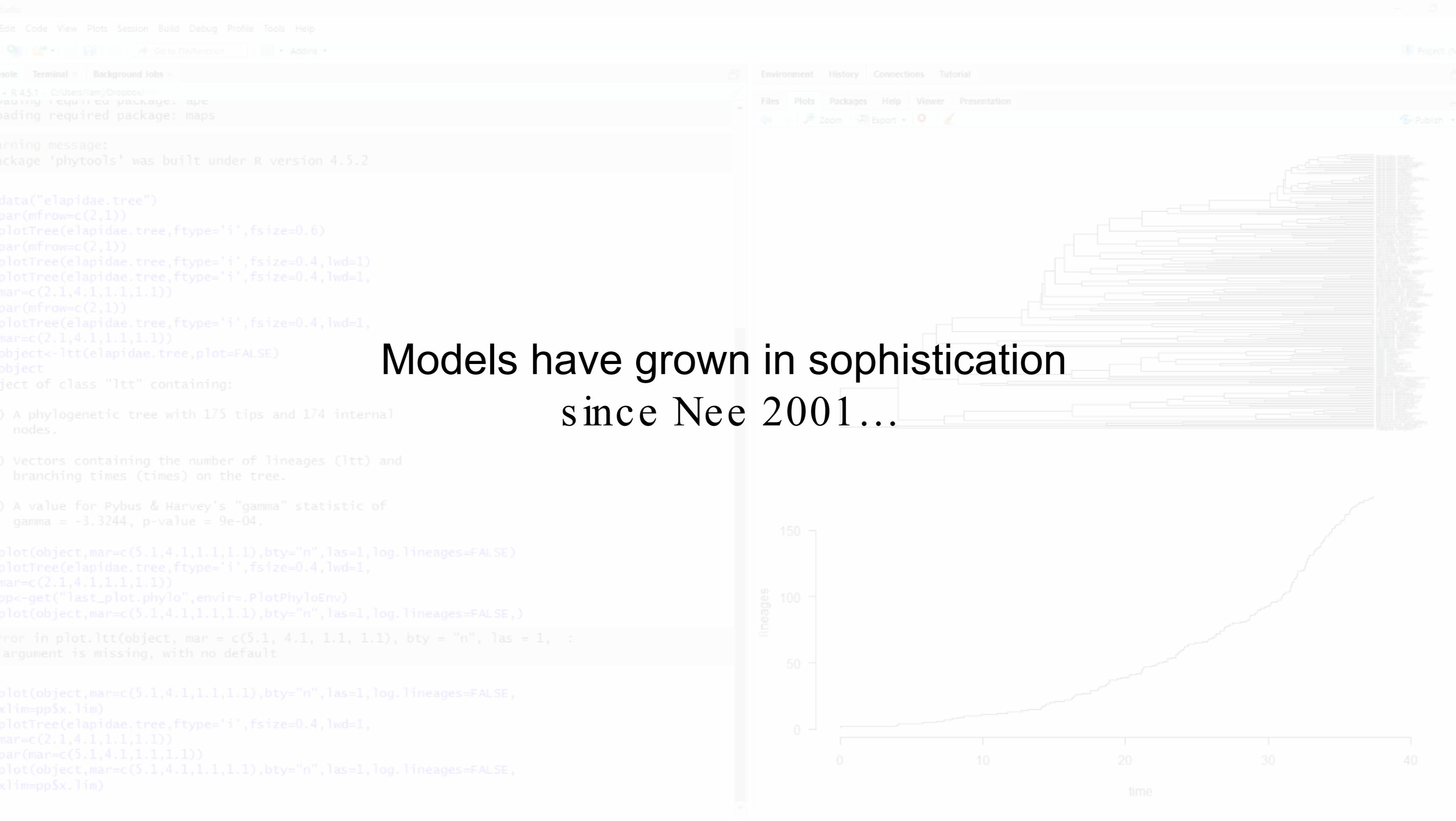
Cusimano N<sup>1</sup>, Stadler T, Renner SS.

```
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE)
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1,
mar=c(2.1,4.1,1.1,1.1))
op<-get("last_plot.phylo",envir=.PlotPhyloEnv)
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE,)

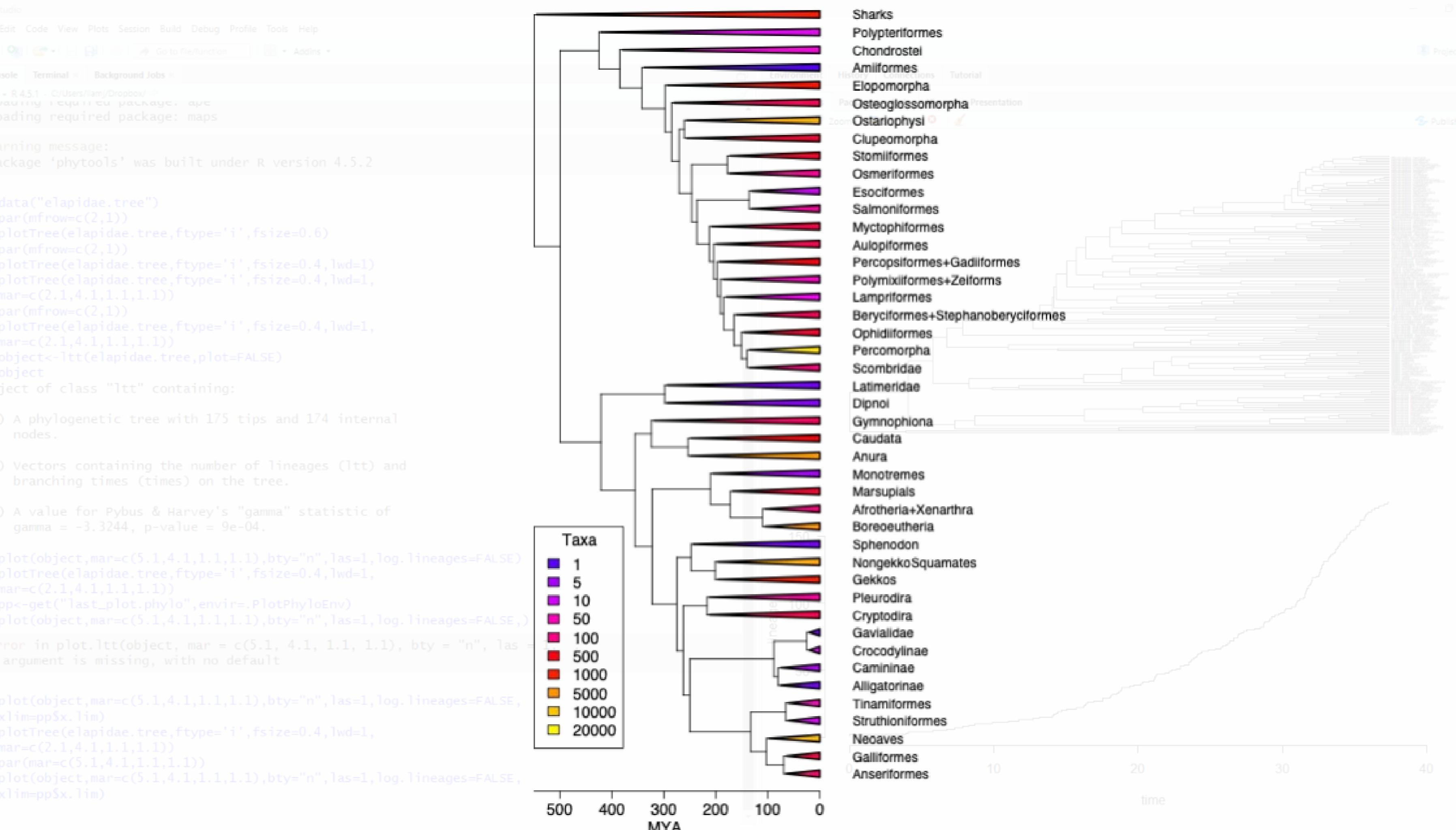
rror in plot.ltt(object, mar = c(5.1, 4.1, 1.1, 1.1), bty = "n", las = 1, :
argument is missing, with no default
```

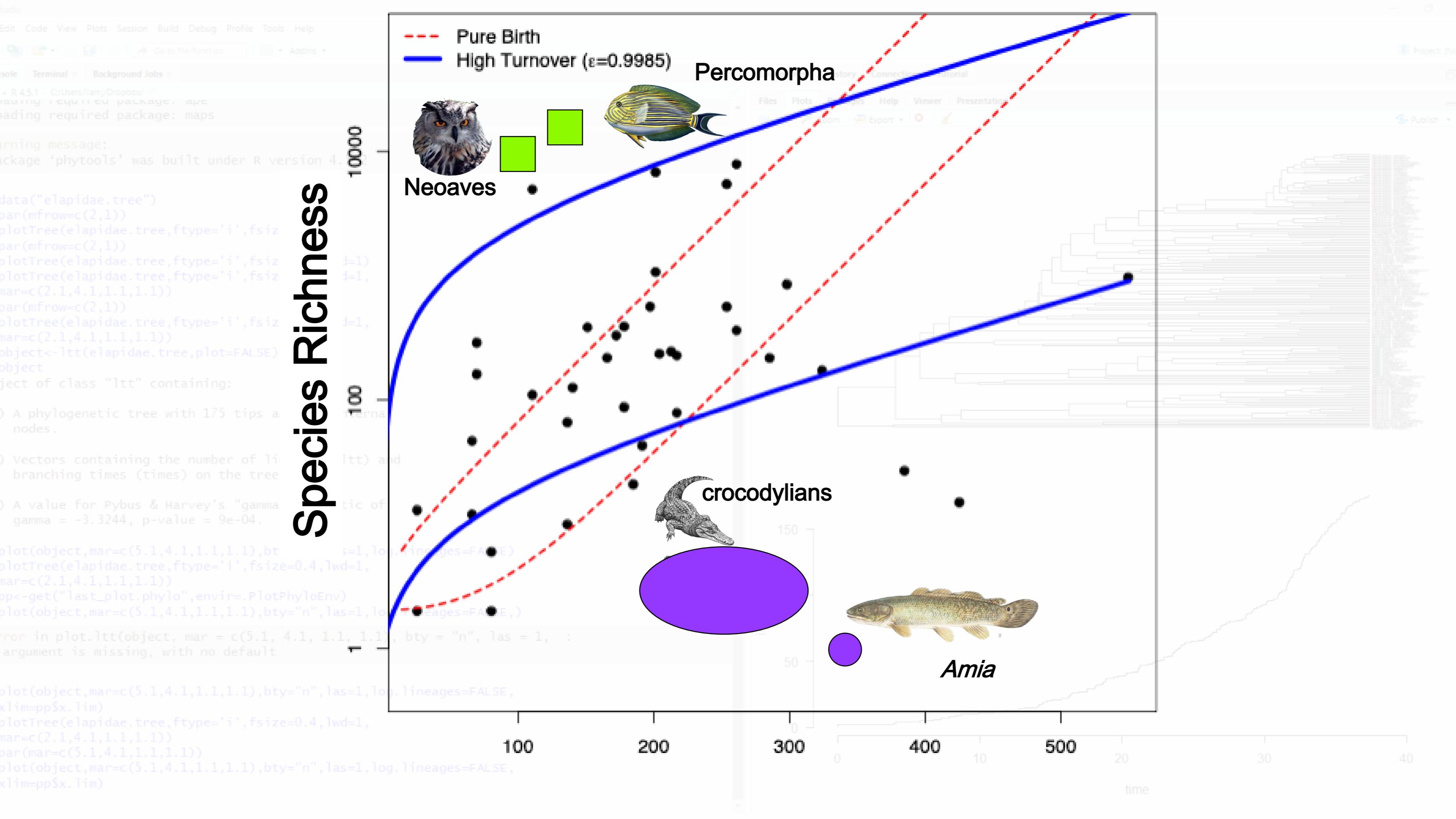
```
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE,
xlim=pp$xFlim)
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1,
mar=c(2.1,4.1,1.1,1.1))
par(mar=c(5.1,4.1,1.1,1.1))
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE,
xlim=pp$xFlim)
```











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Console Terminal > Background Jobs >

R 4.5.1 - C:/Users/lamj/Dropbox/

Warning message:

package 'phytools' was built

```
data("elapidae.tree")
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype="rect")
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype="rect")
plotTree(elapidae.tree,ftype="rect")
mar=c(2.1,4.1,1.1,1.1))
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype="rect")
mar=c(2.1,4.1,1.1,1.1))
object<-ltt(elapidae.tree,plot=TRUE)
object
object of class "ltt" containing
```

) A phylogenetic tree with 1 nodes.

) Vectors containing the number of branching times (times) or

) A value for Pybus & Harvey gamma = -3.3244, p-value =

```
plot(object,mar=c(5.1,4.1,1,1))
plotTree(elapidae.tree,ftype="rect")
mar=c(2.1,4.1,1.1,1.1))
op<-get("last_plot.phylo",envir=pp)
plot(object,mar=c(5.1,4.1,1,1))
error in plot.ltt(object, mar = 1) : argument "x" is missing, with n
```

```
plot(object,mar=c(5.1,4.1,1,1))
xlim=pp$xFlim)
plotTree(elapidae.tree,ftype="rect")
mar=c(2.1,4.1,1.1,1.1))
par(mar=c(5.1,4.1,1.1,1.1))
plot(object,mar=c(5.1,4.1,1,1))
xlim=pp$xFlim)
```



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R 4.5.1 - C:/Users/lamj/Dropbox/  
Loading required package: maps

Warning message:  
package 'phytools' was built under R version 4.5.2

```
data("elapidae.tree")
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fsize=0.6)
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1)
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1,
mar=c(2.1,4.1,1.1,1.1))
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1,
mar=c(2.1,4.1,1.1,1.1))
object<-ltt(elapidae.tree,plot=FALSE)
object
```

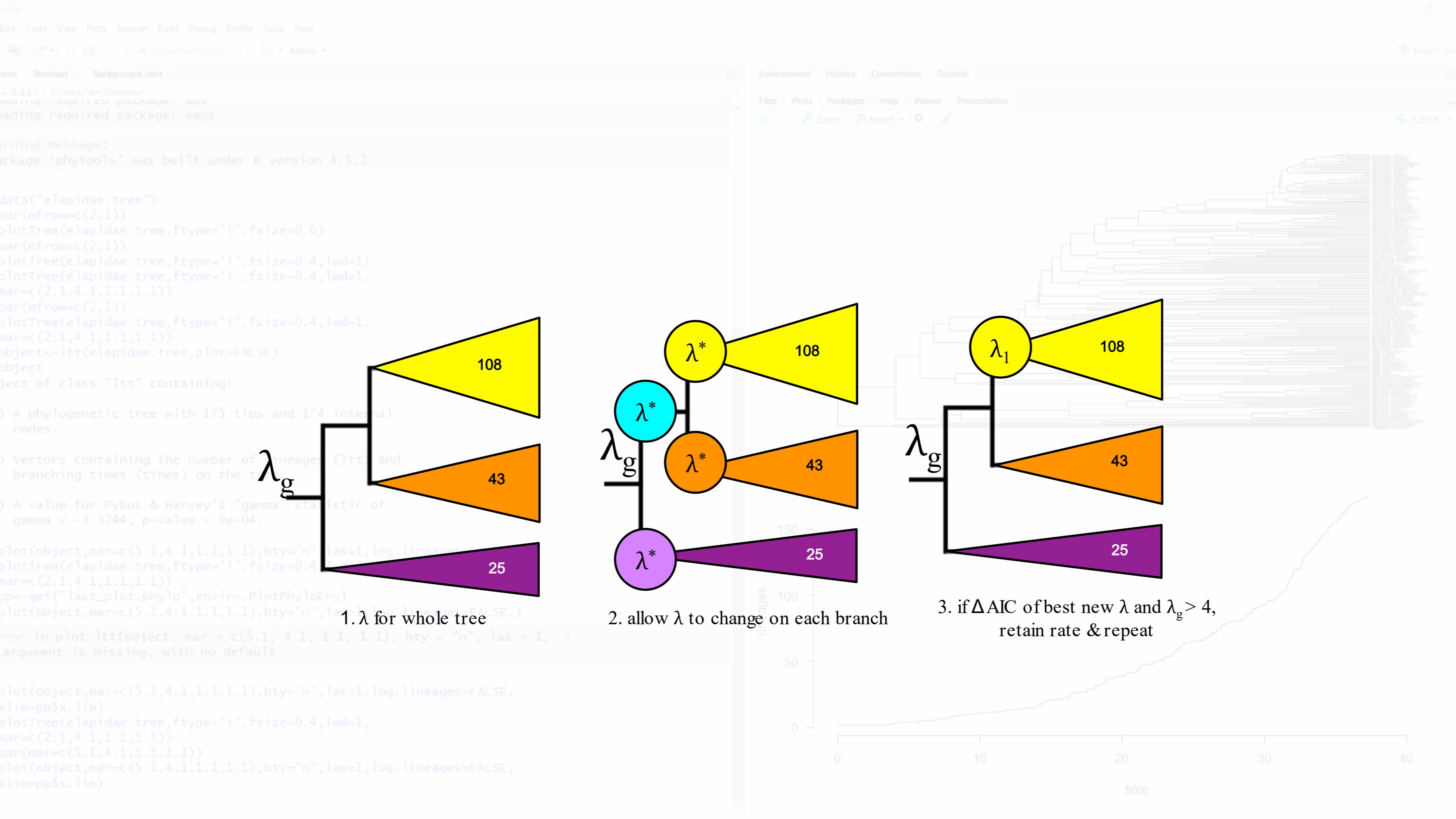
object of class "ltt" containing:

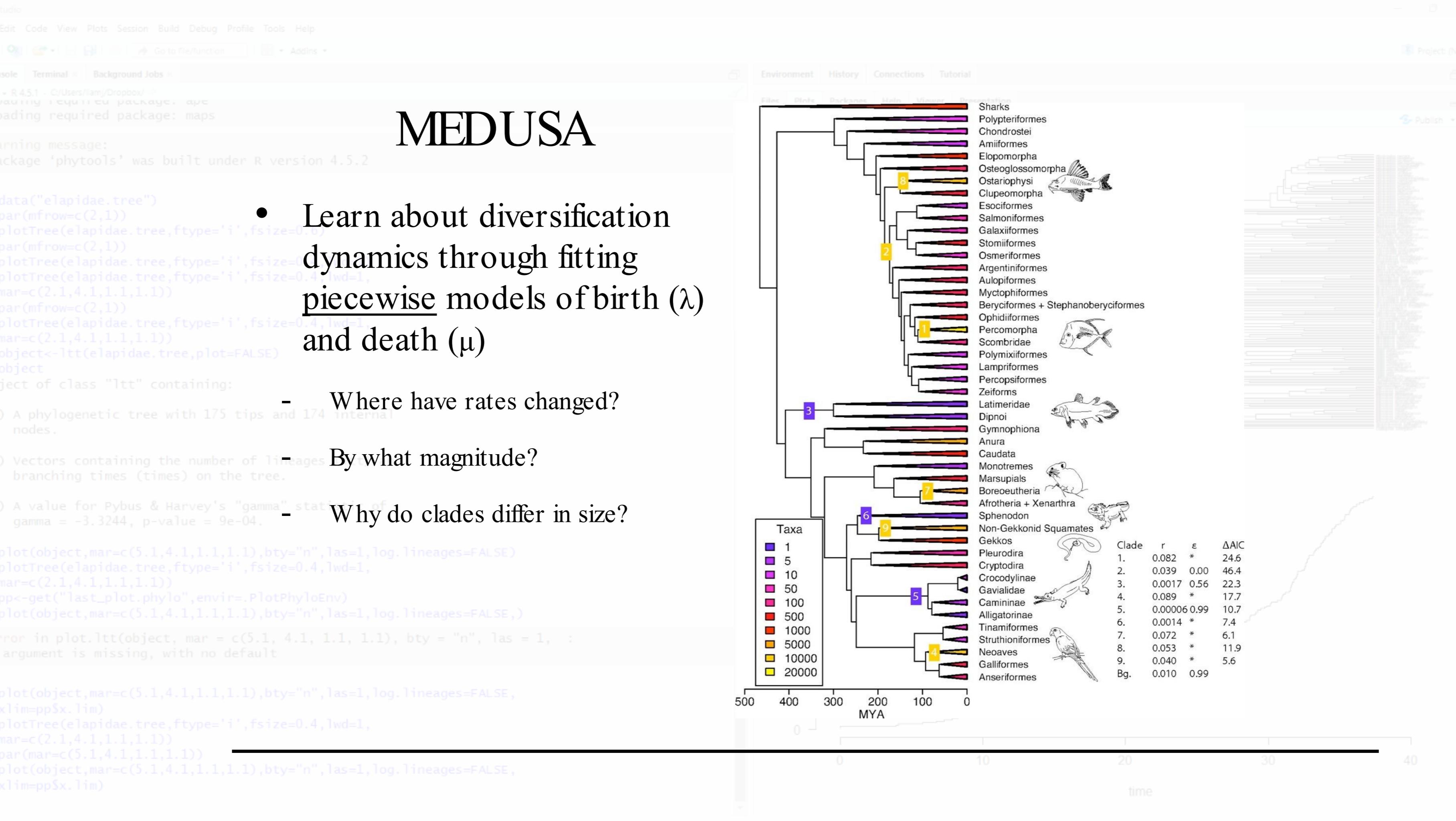
- ) A phylogenetic tree with 175 tips and 174 internal nodes.
- ) Vectors containing the number of lineages (ltt) and branching times (times) on the tree.
- ) A value for Pybus & Harvey's "gamma" statistic of gamma = -3.3244, p-value = 9e-04.

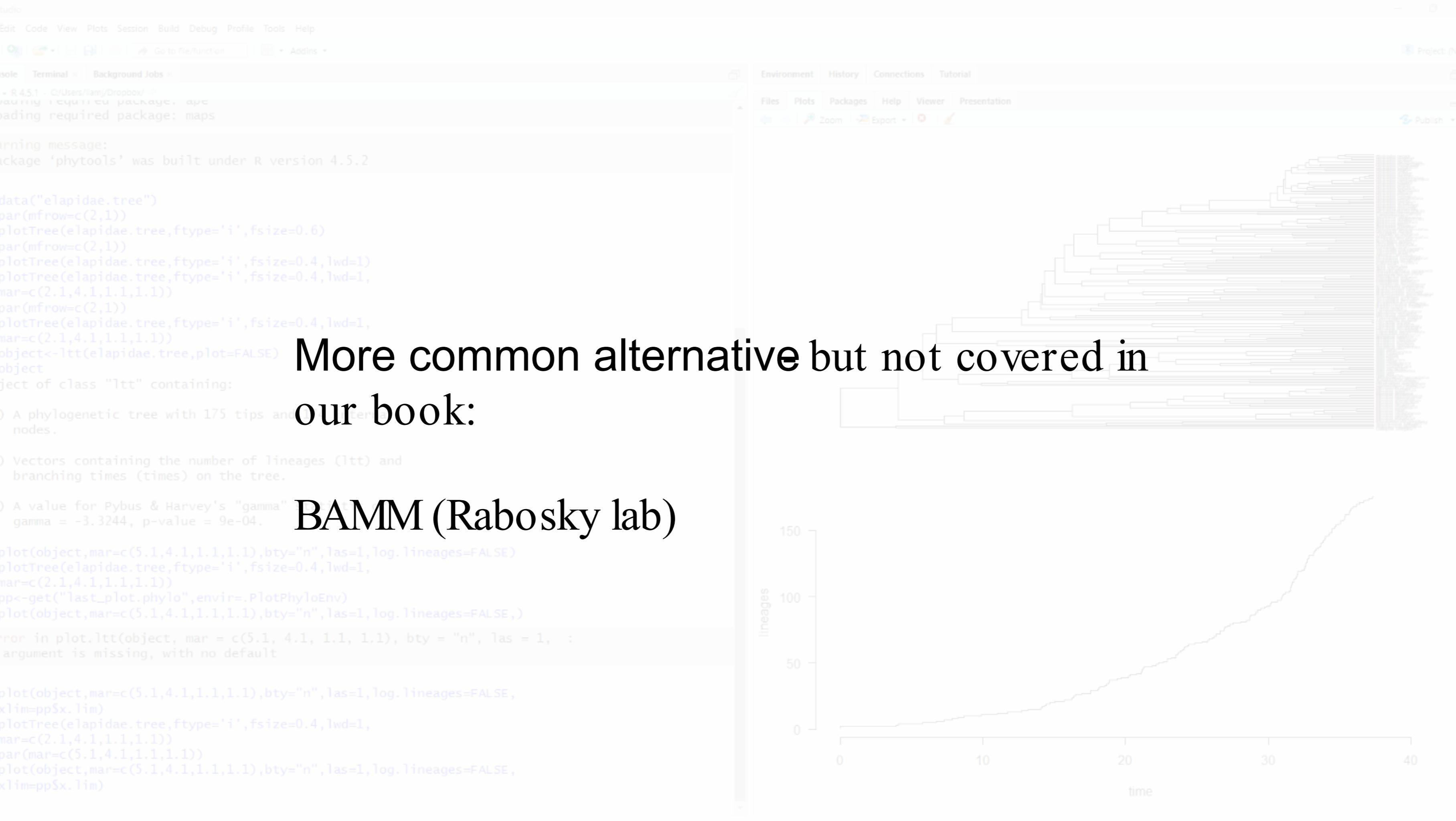
```
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE)
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1,
mar=c(2.1,4.1,1.1,1.1))
op<-get("last_plot.phylo",envir=.PlotPhyloEnv)
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE)
error in plot.ltt(object, mar = c(5.1, 4.1, 1.1, 1.1), bty = "n", las = 1) :
  argument is missing, with no default
```

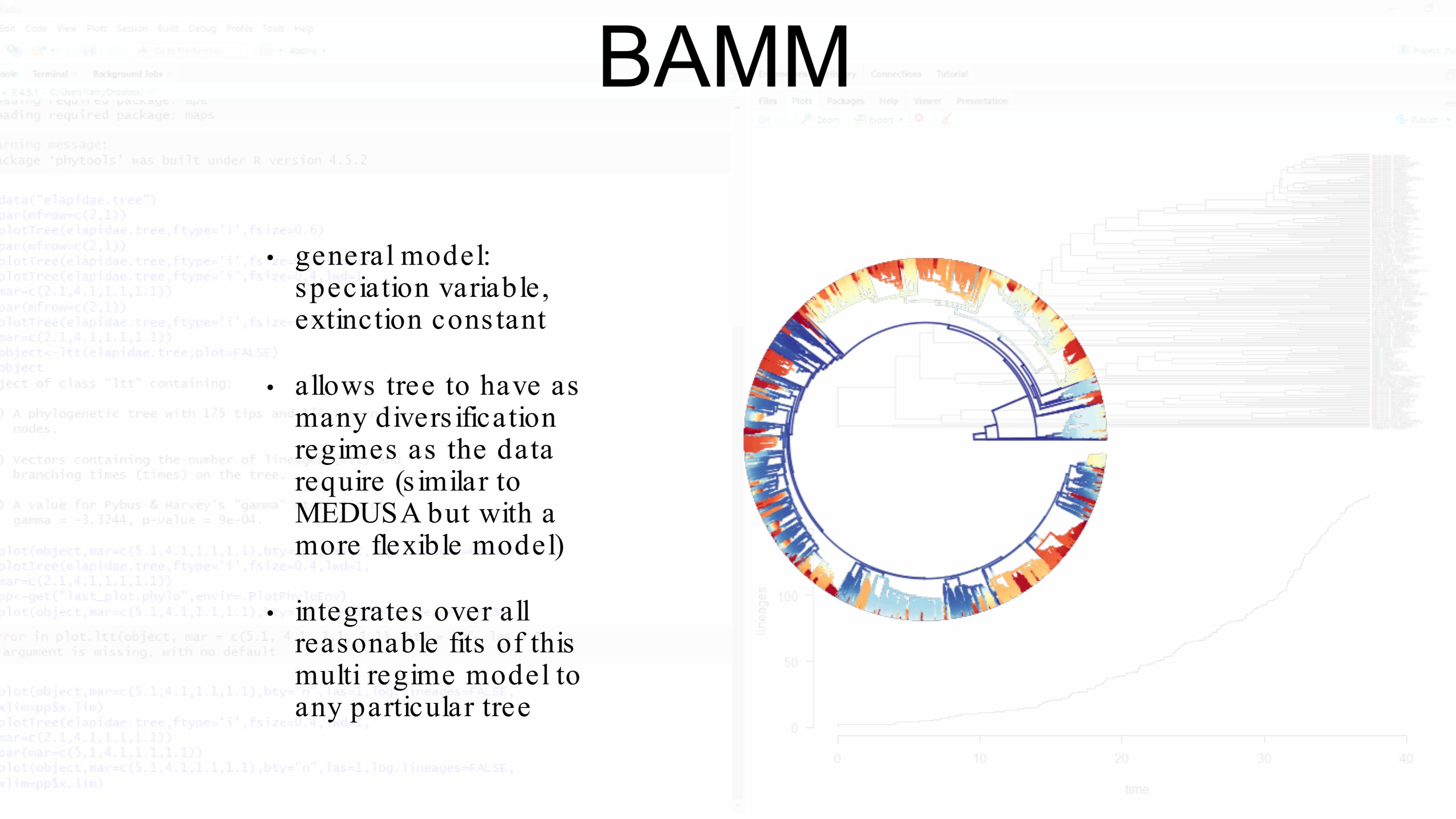
```
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE)
xlim=pp$xElim)
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1,
mar=c(2.1,4.1,1.1,1.1))
par(mar=c(5.1,4.1,1.1,1.1))
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log.lineages=FALSE)
xlim=pp$xElim)
```

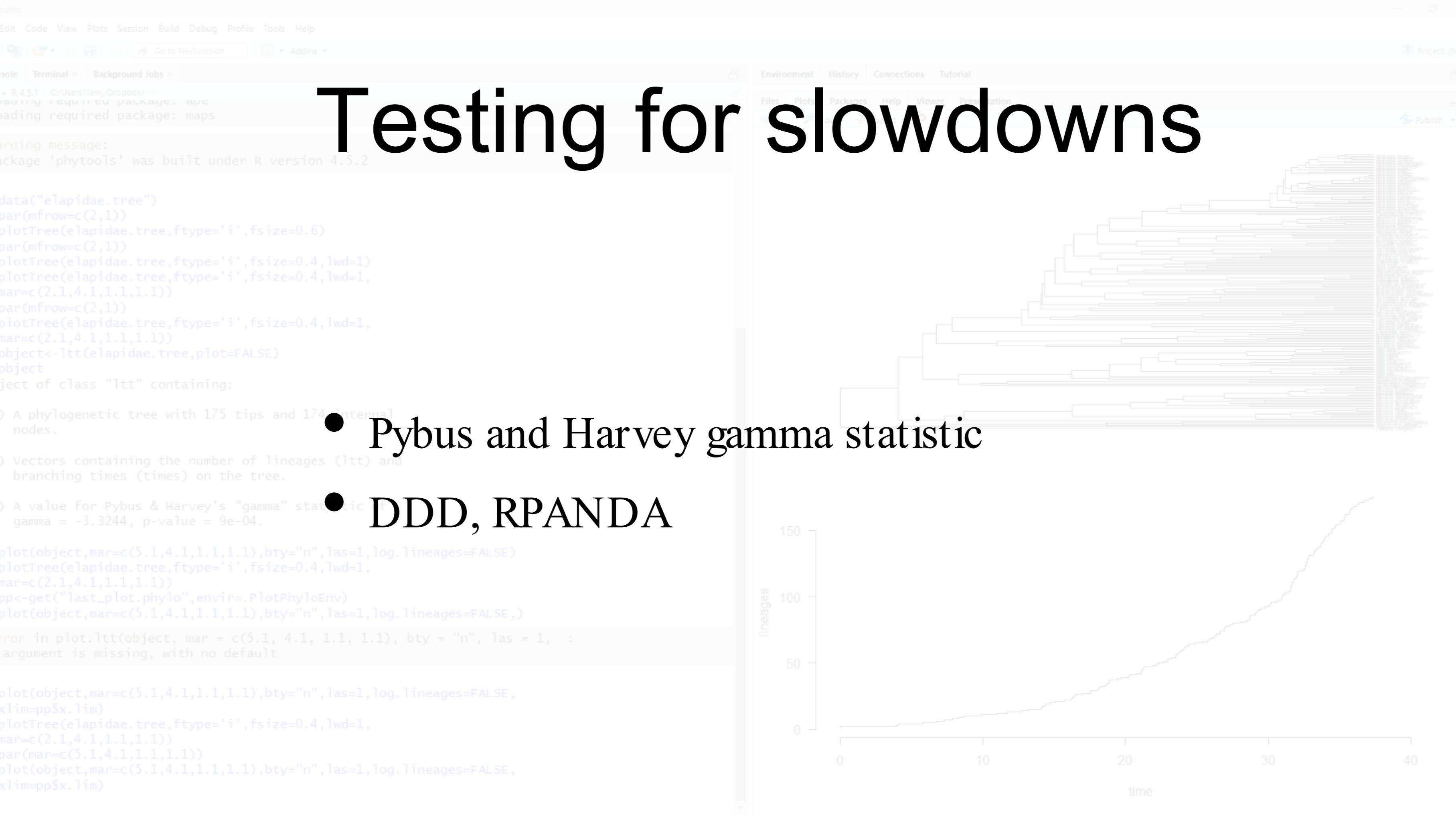


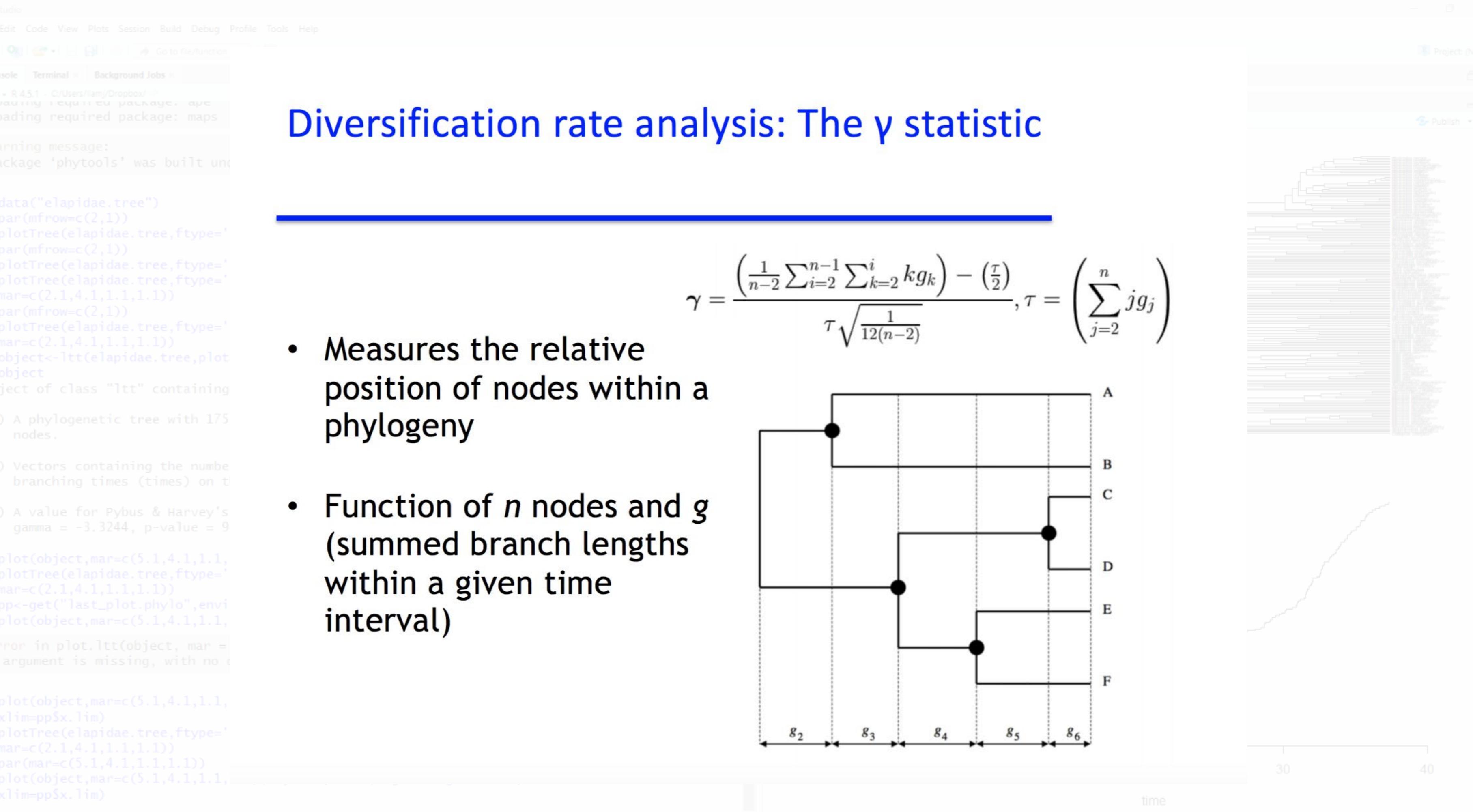


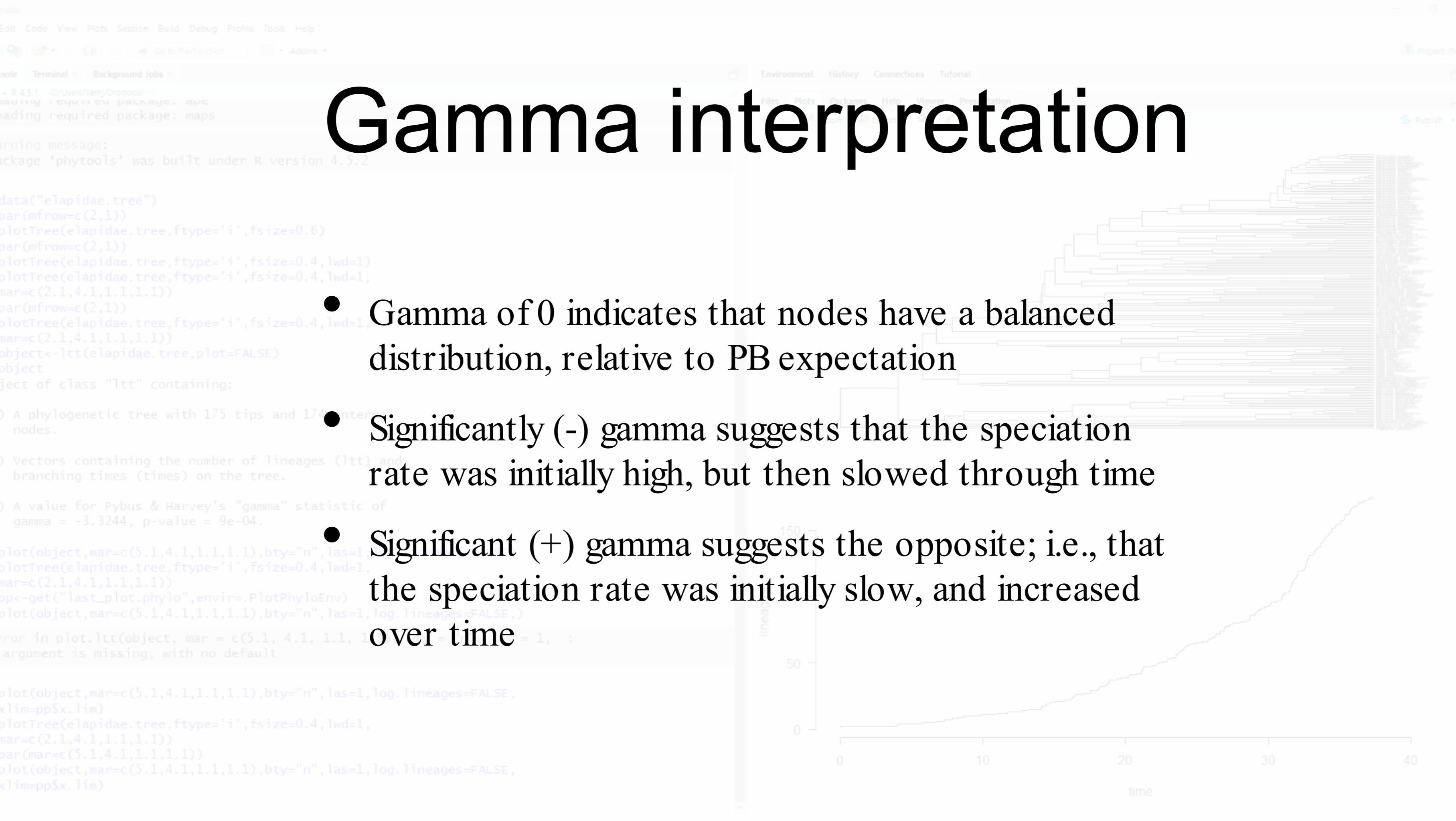


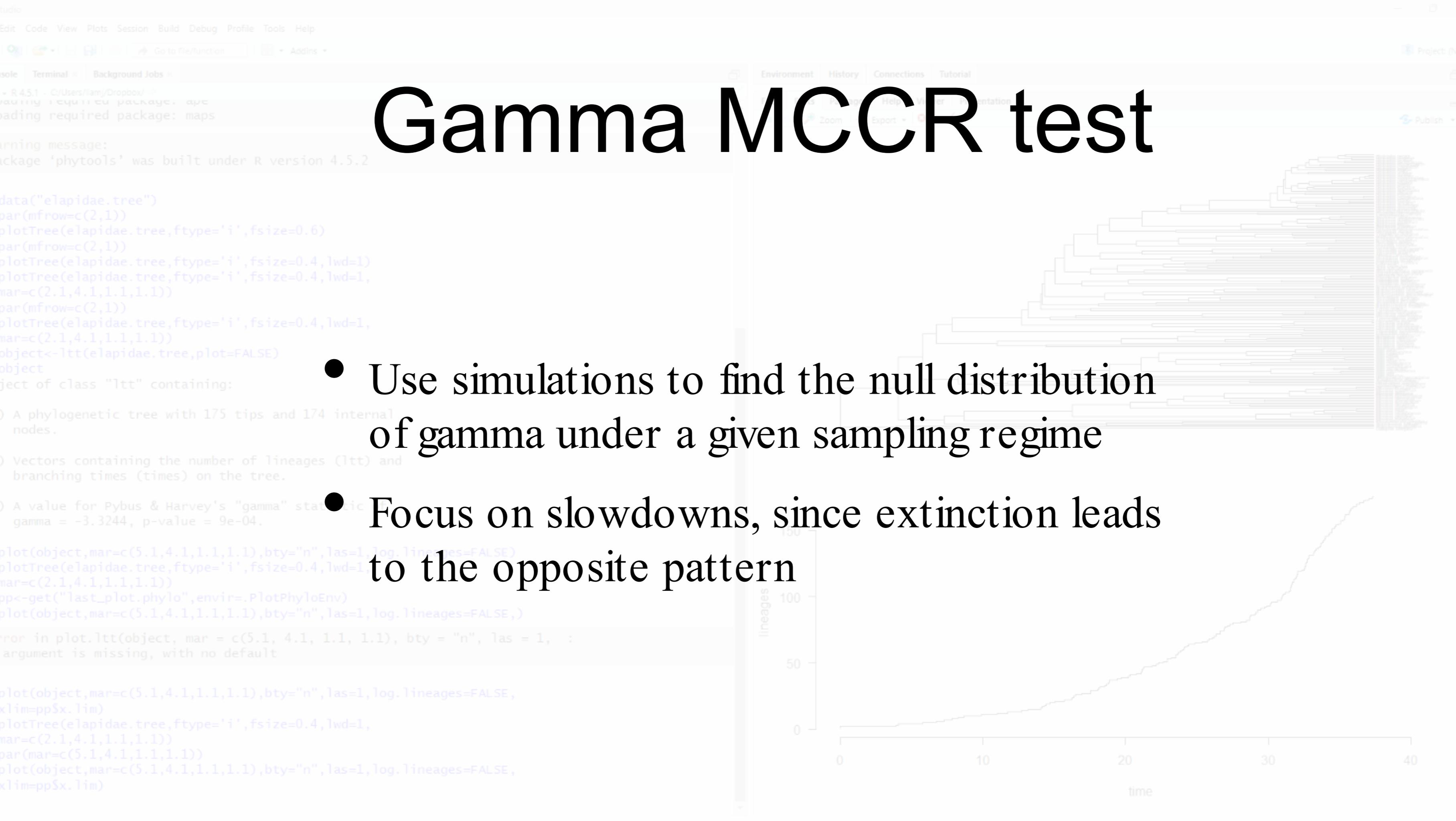


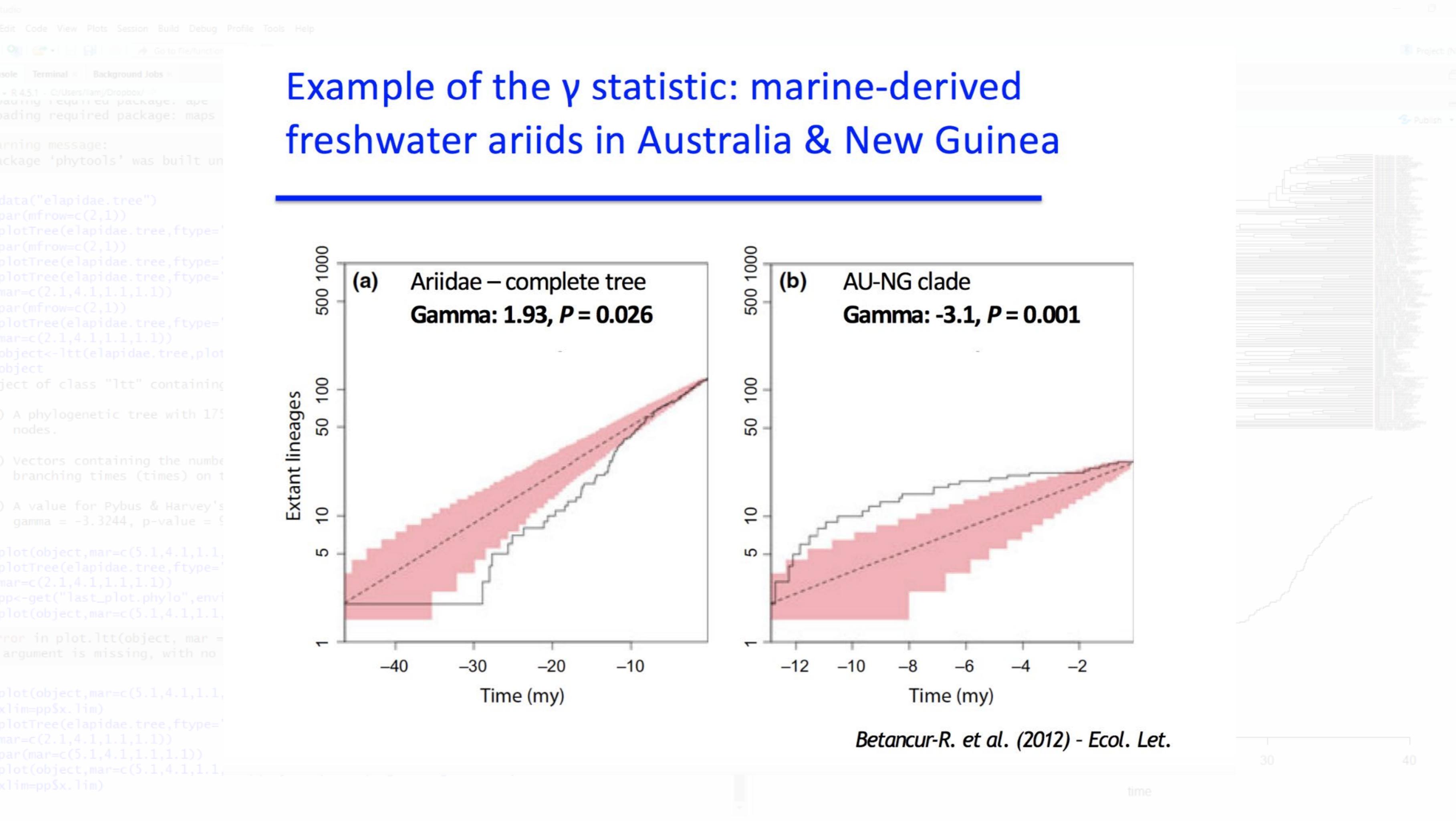




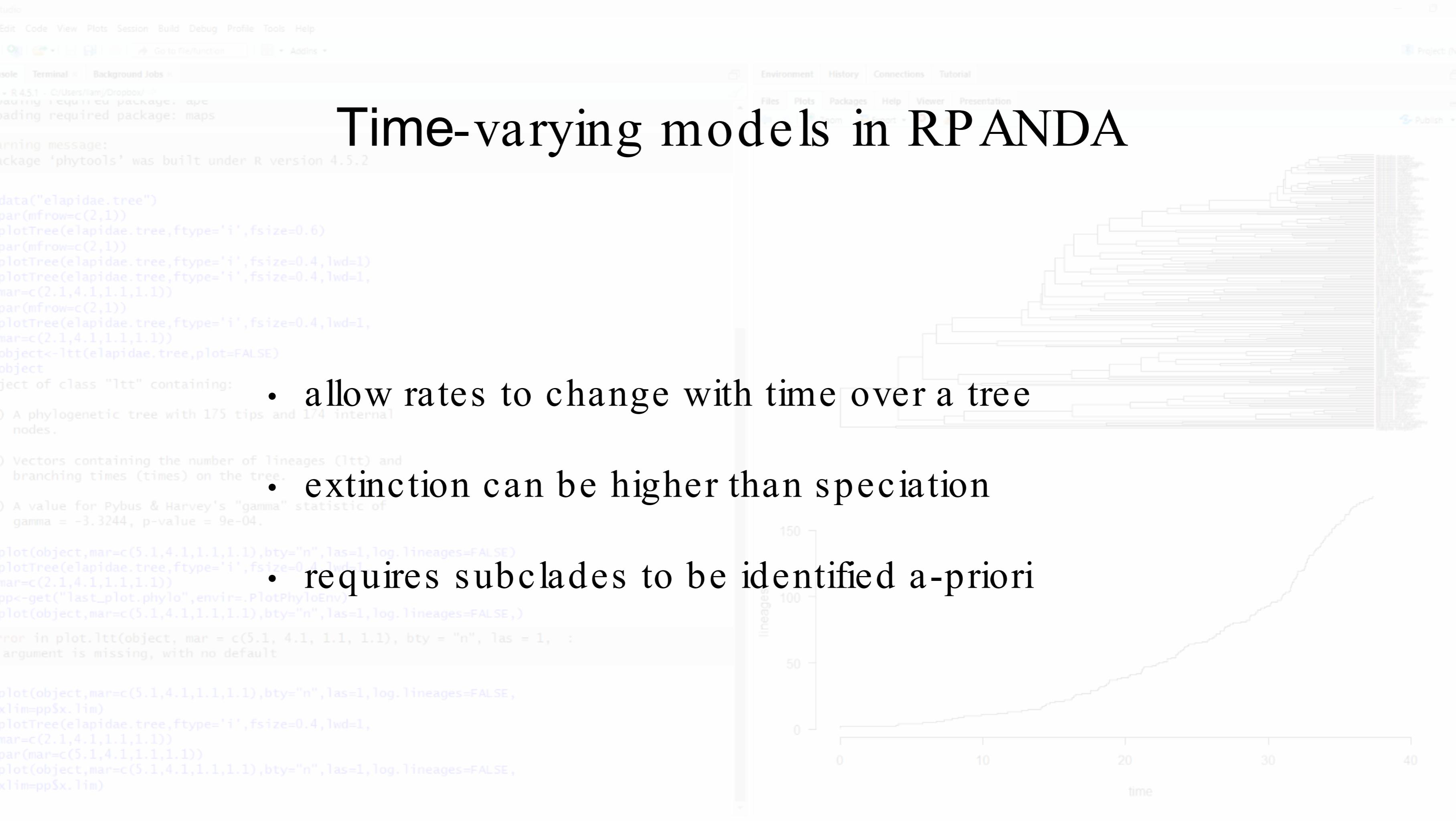


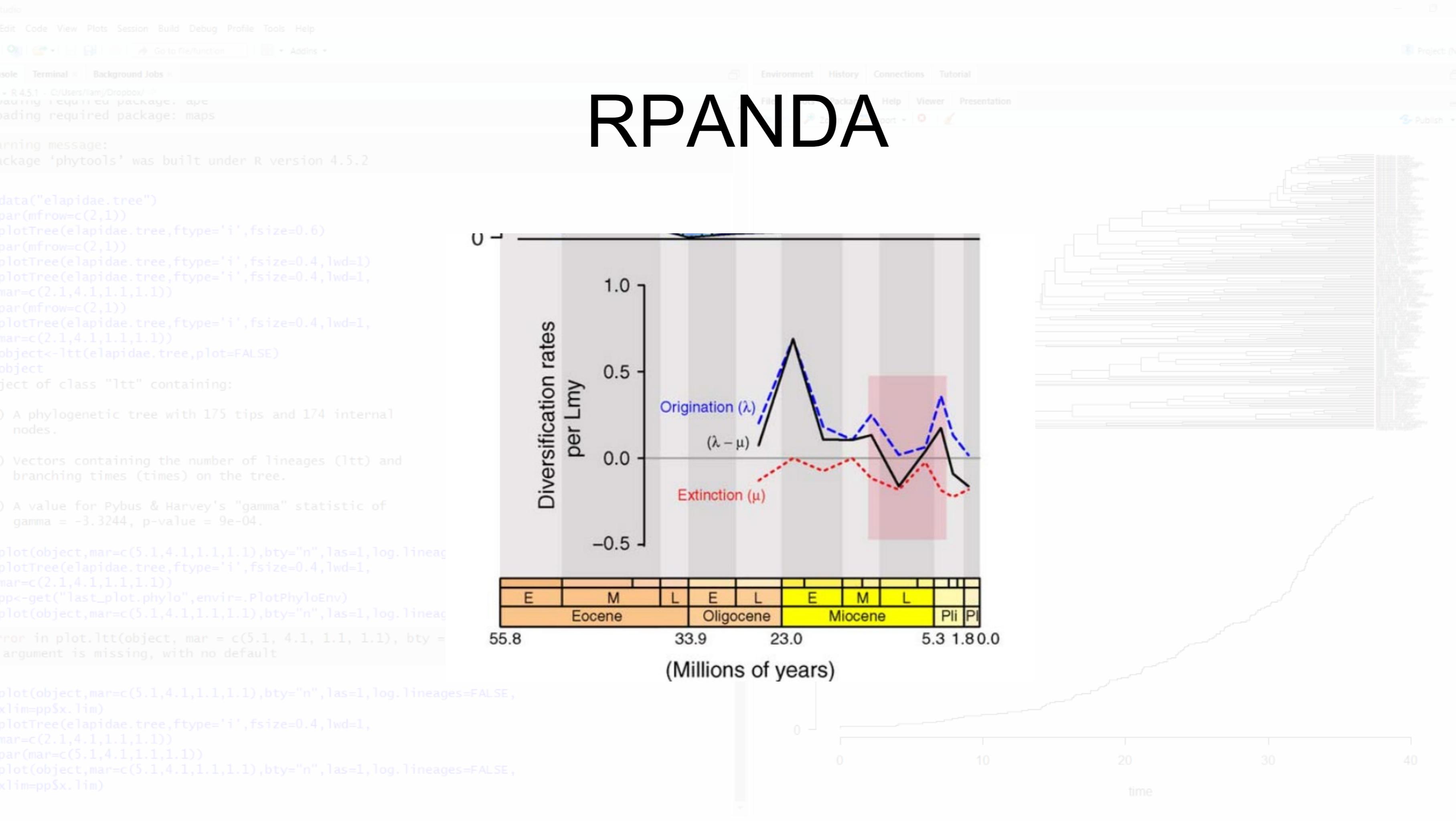












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File Project Go to File/Function

Console Terminal > Background Jobs >

R 4.5.1 - C:/Users/lamj/Dropbox/...  
Warning: required package: ape  
Loading required package: maps

Warning message:  
package 'phytools' was built under R

```
data("elapidae.tree")
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fs=1)
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fs=1)
plotTree(elapidae.tree,ftype='i',fs=1,mar=c(2.1,4.1,1.1,1.1))
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fs=1,mar=c(2.1,4.1,1.1,1.1))
object<-ltt(elapidae.tree,plot=FALSE)
object
```

Object of class "ltt" containing:

A phylogenetic tree with 175 tips  
nodes.

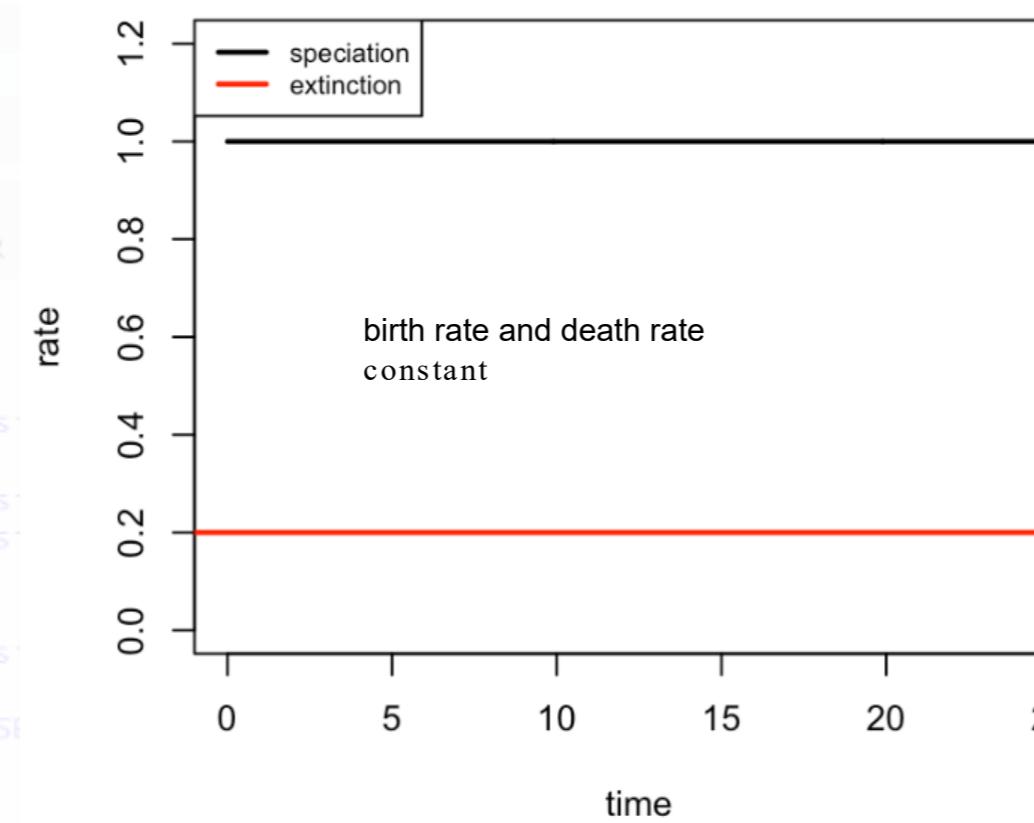
Vectors containing the number of  
branching times (times) on the tree

A value for Pybus & Harvey's "gammr"  
gamma = -3.3244, p-value = 9e-04.

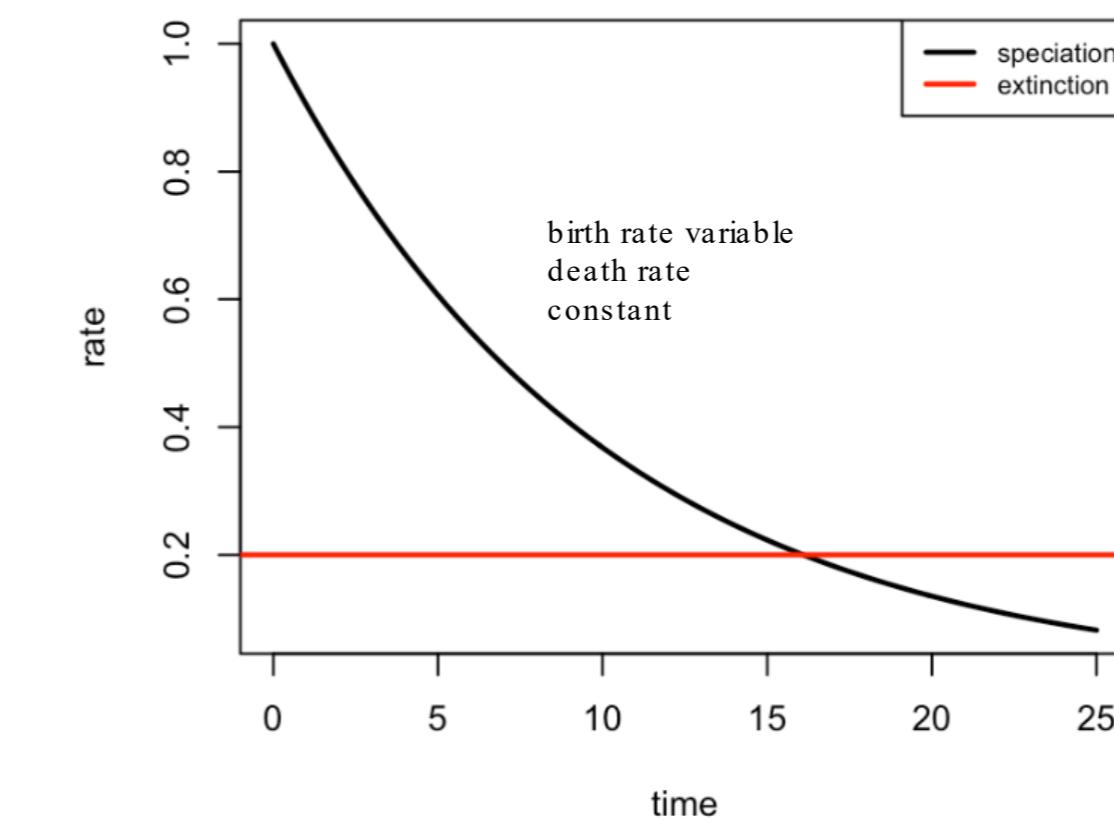
```
plot(object,mar=c(5.1,4.1,1.1,1.1),l
plotTree(elapidae.tree,ftype='i',fs=1,
mar=c(2.1,4.1,1.1,1.1))
op<-get("last_plot.phylo",envir=PlotEnv)
plot(object,mar=c(5.1,4.1,1.1,1.1),l
error in plot.ltt(object, mar = c(5.1
argument is missing, with no default
```

```
plot(object,mar=c(5.1,4.1,1.1,1.1),l
xlim=pp$xF.ylim)
plotTree(elapidae.tree,ftype='i',fs=1,
mar=c(2.1,4.1,1.1,1.1))
par(mar=c(5.1,4.1,1.1,1.1))
plot(object,mar=c(5.1,4.1,1.1,1.1),l
xlim=pp$xF.ylim)
```

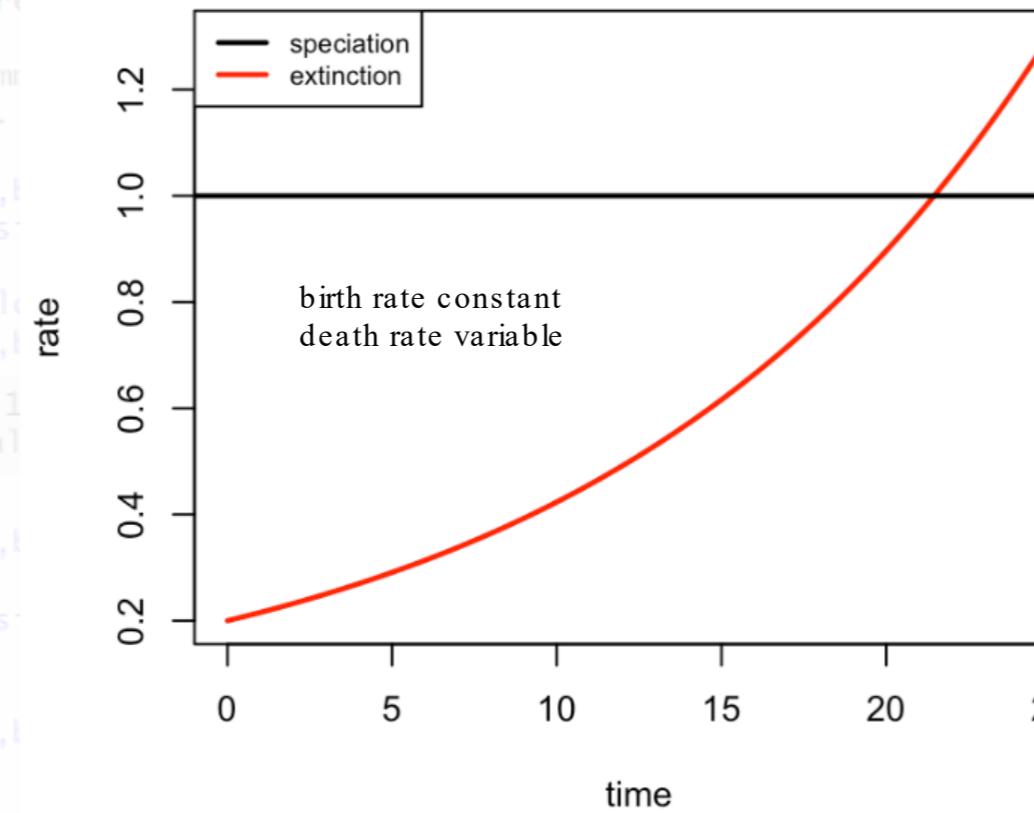
## BCSTD CST



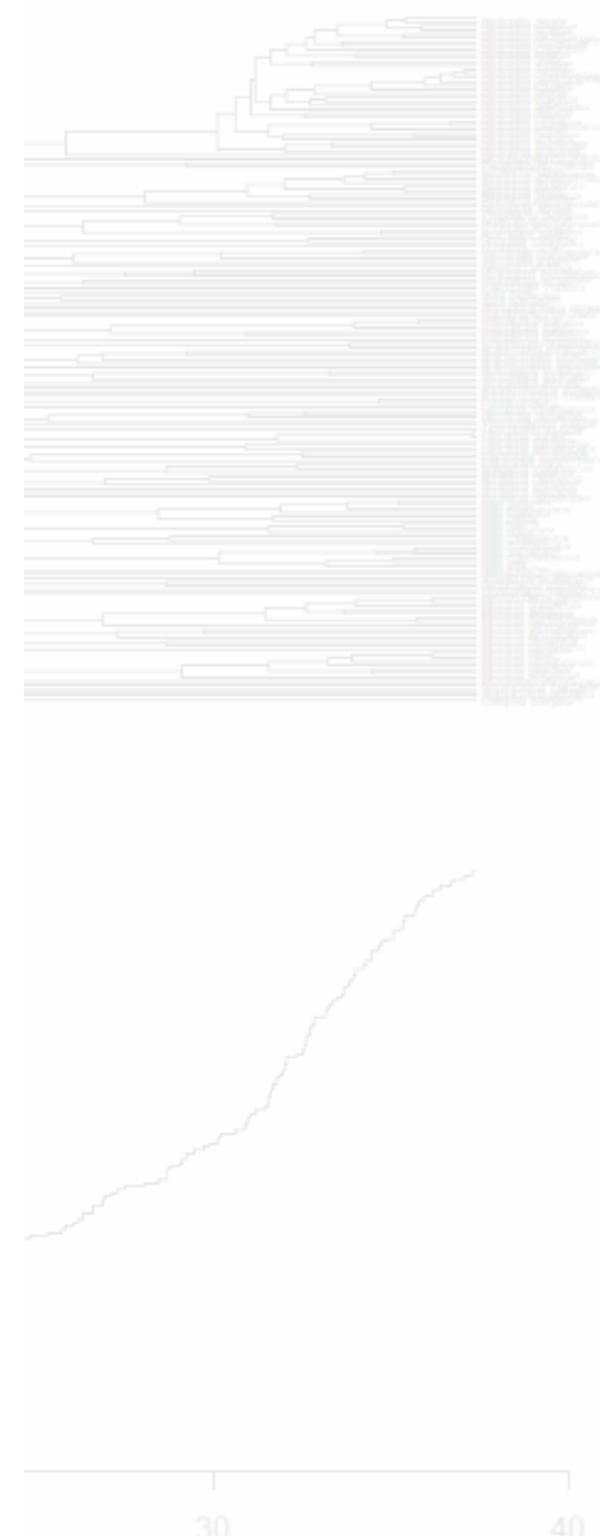
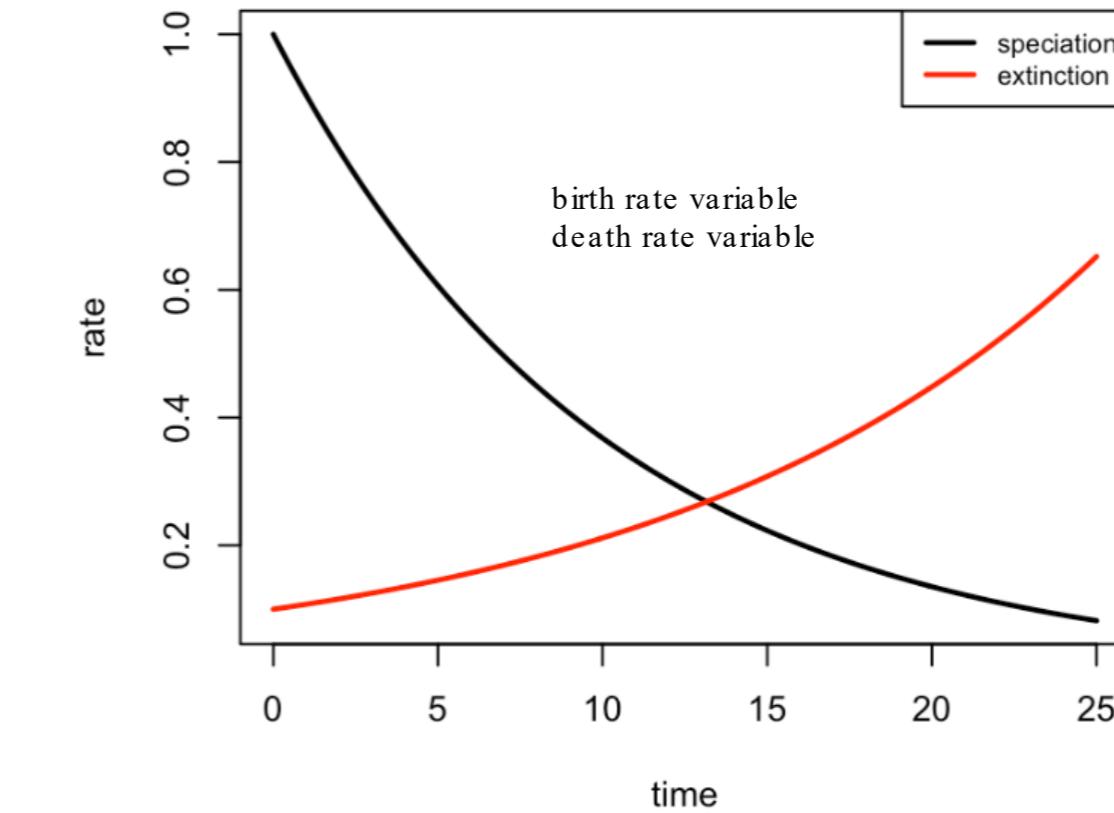
## BVAR DCST

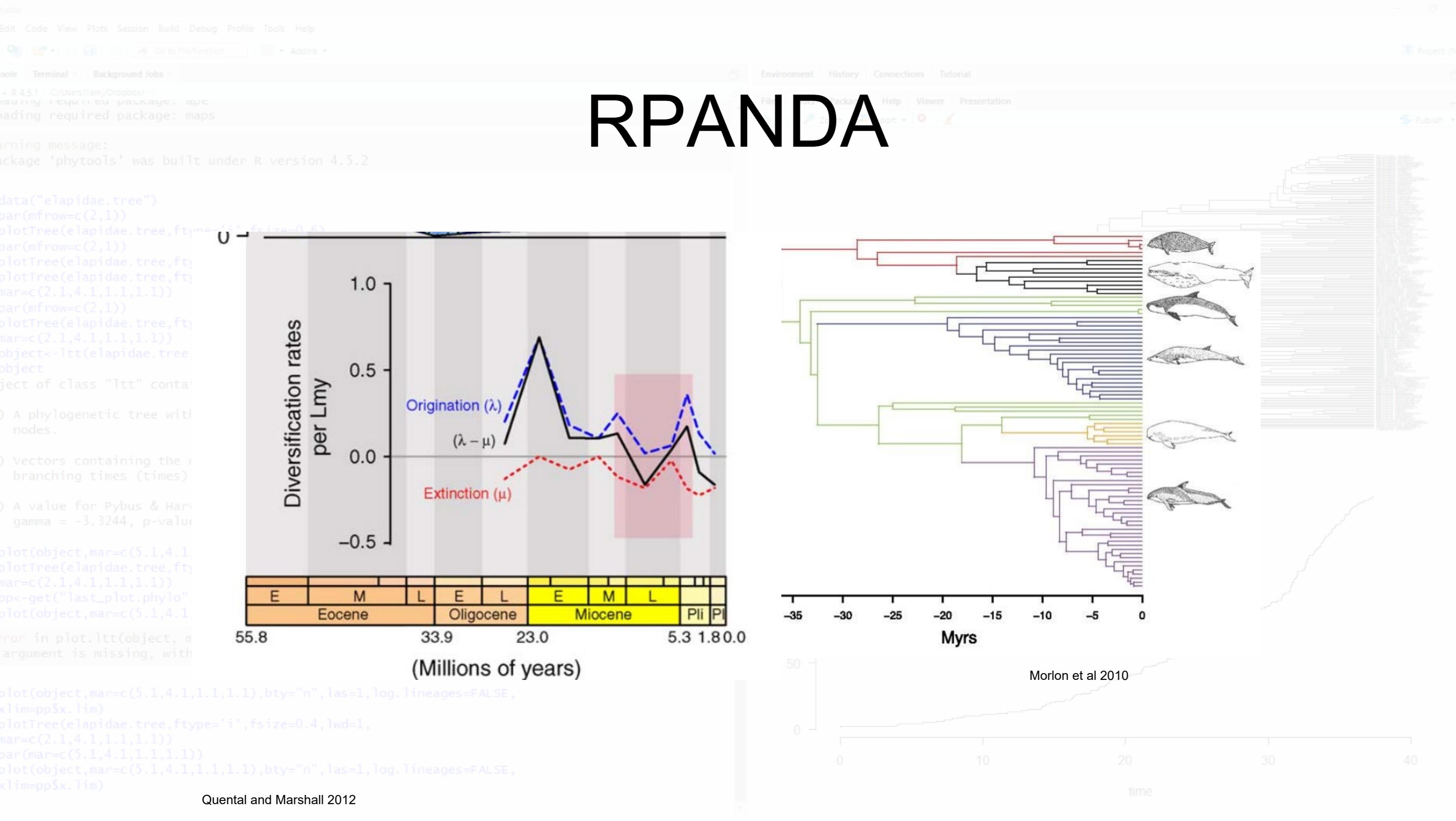


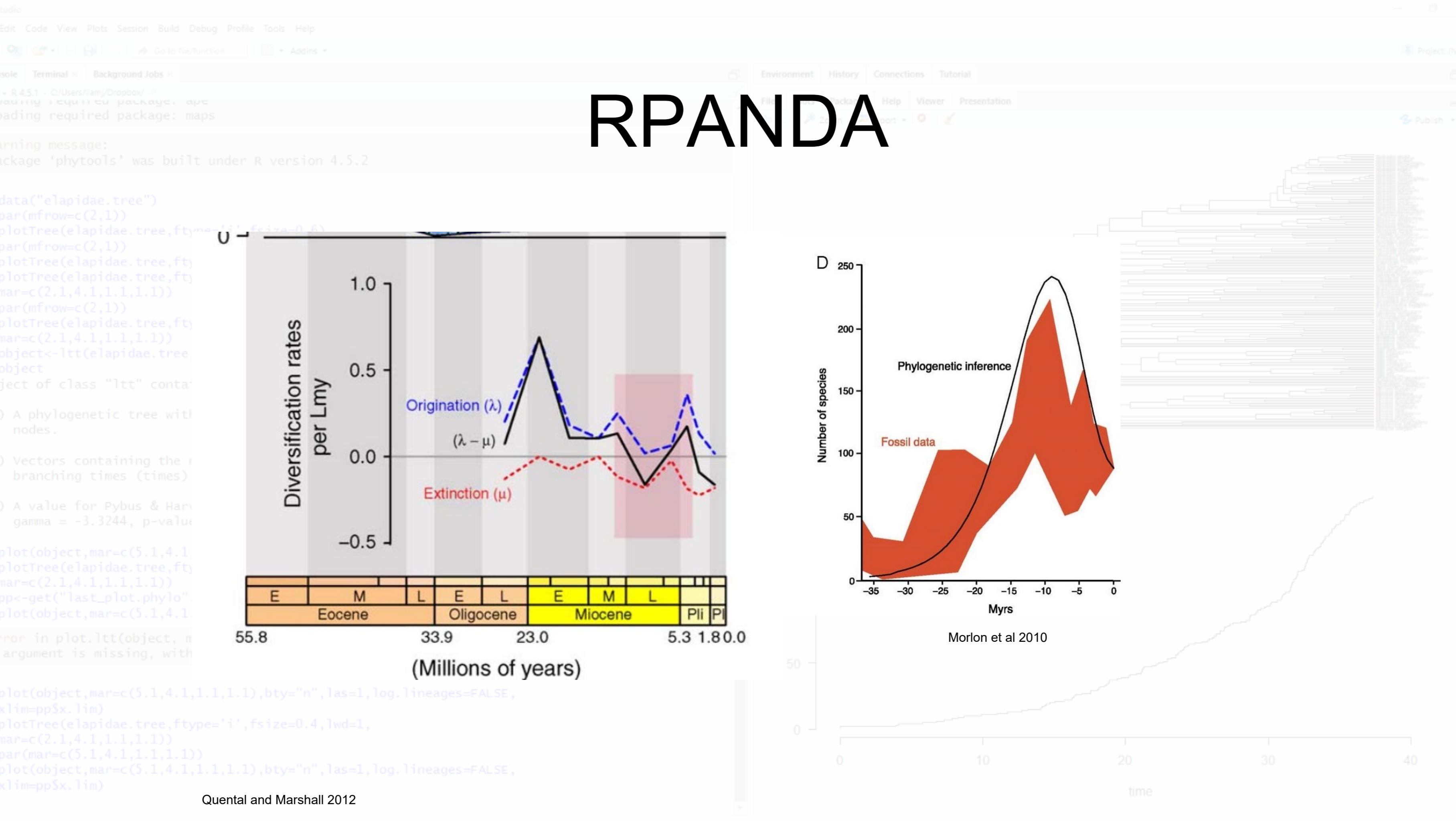
## BCSTD VAR



## BVAR D VAR

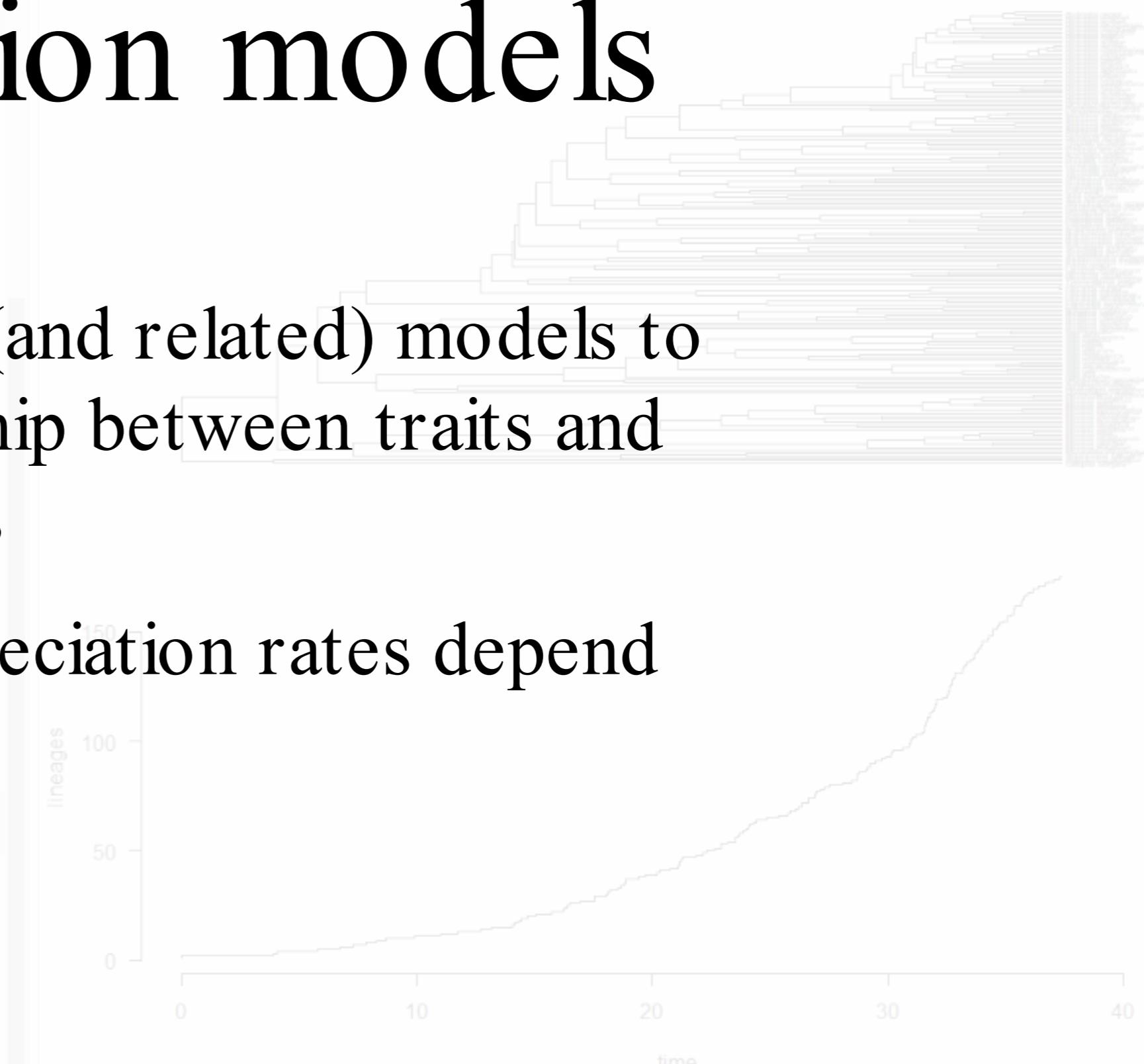


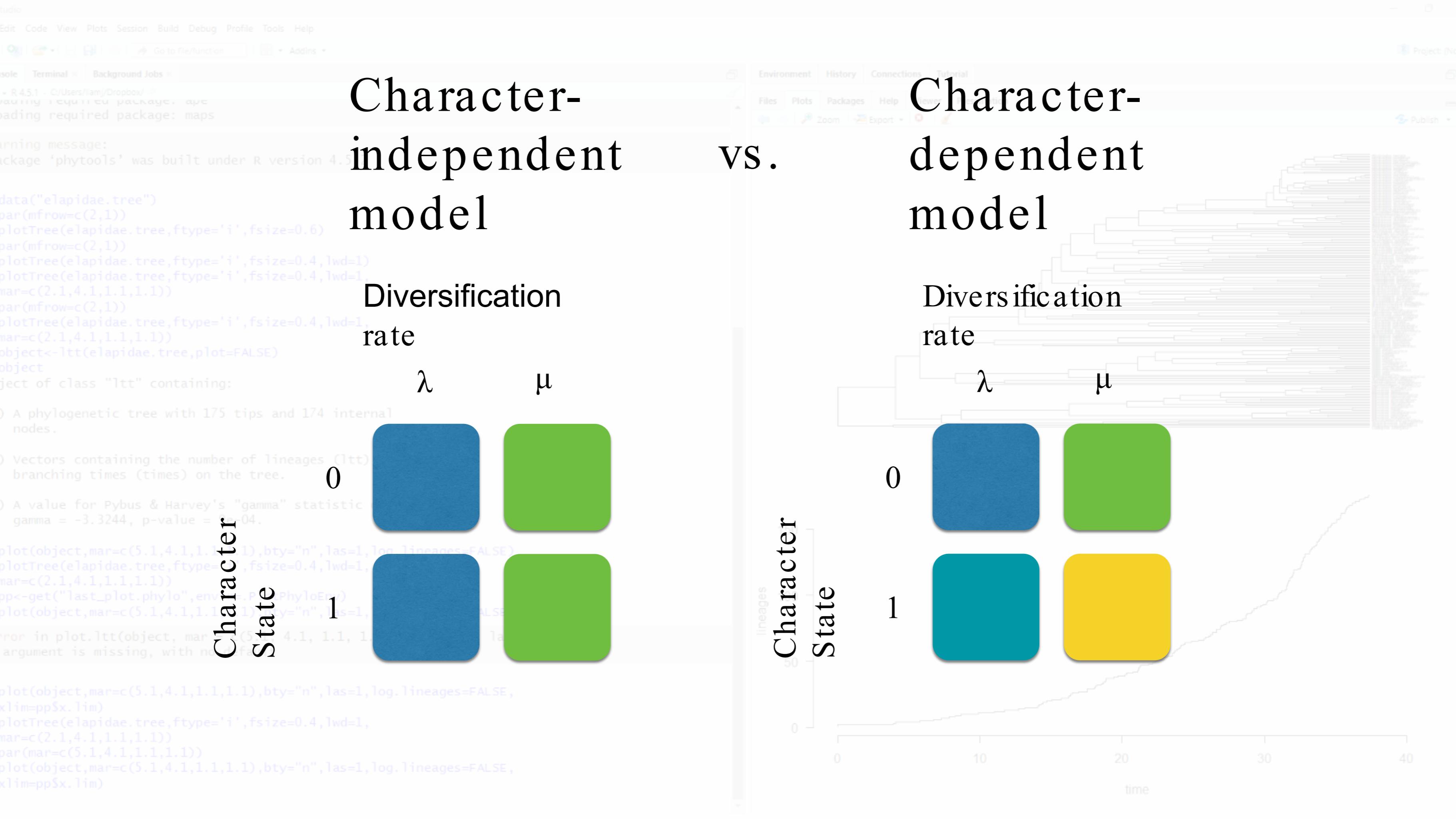


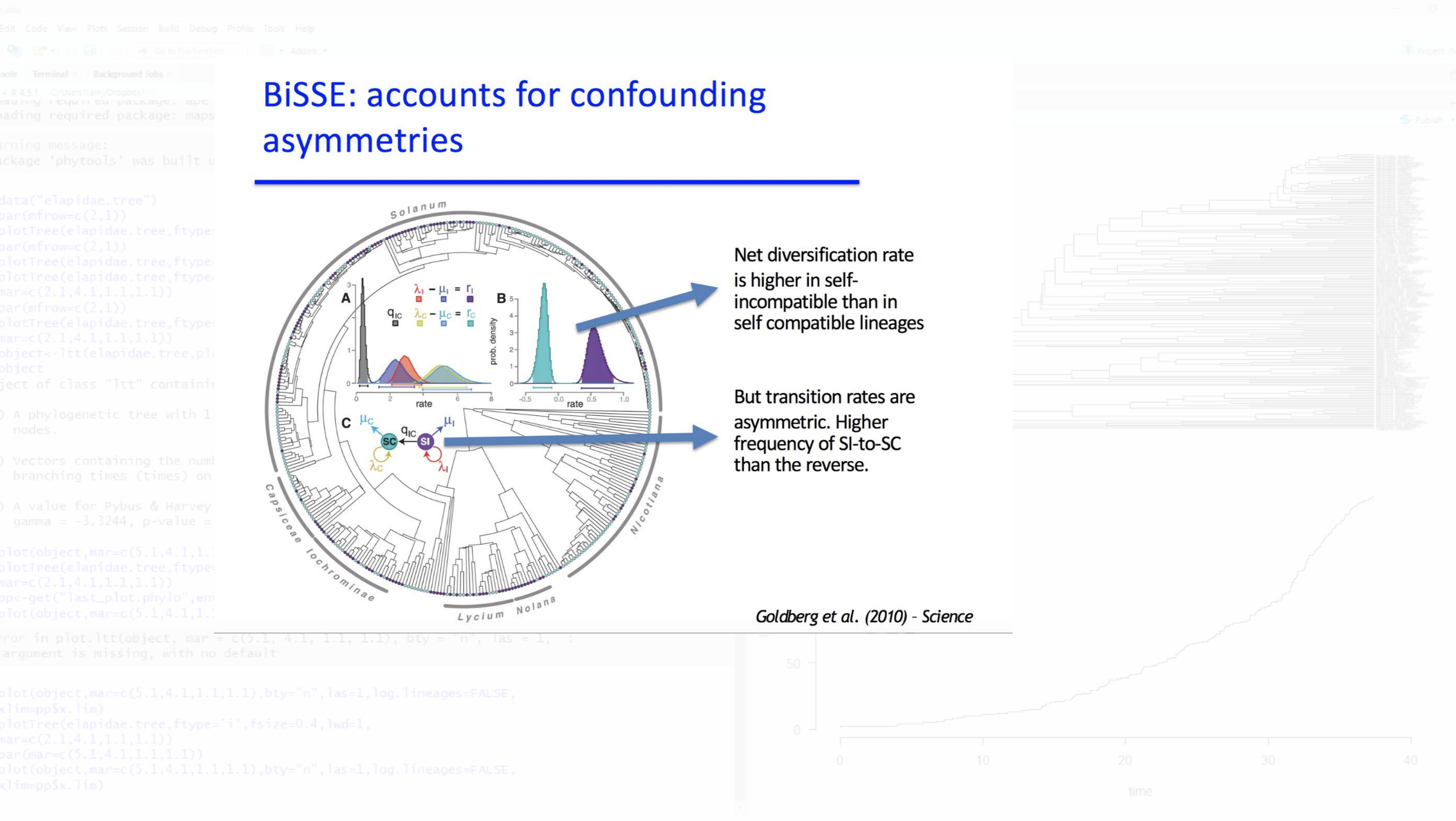


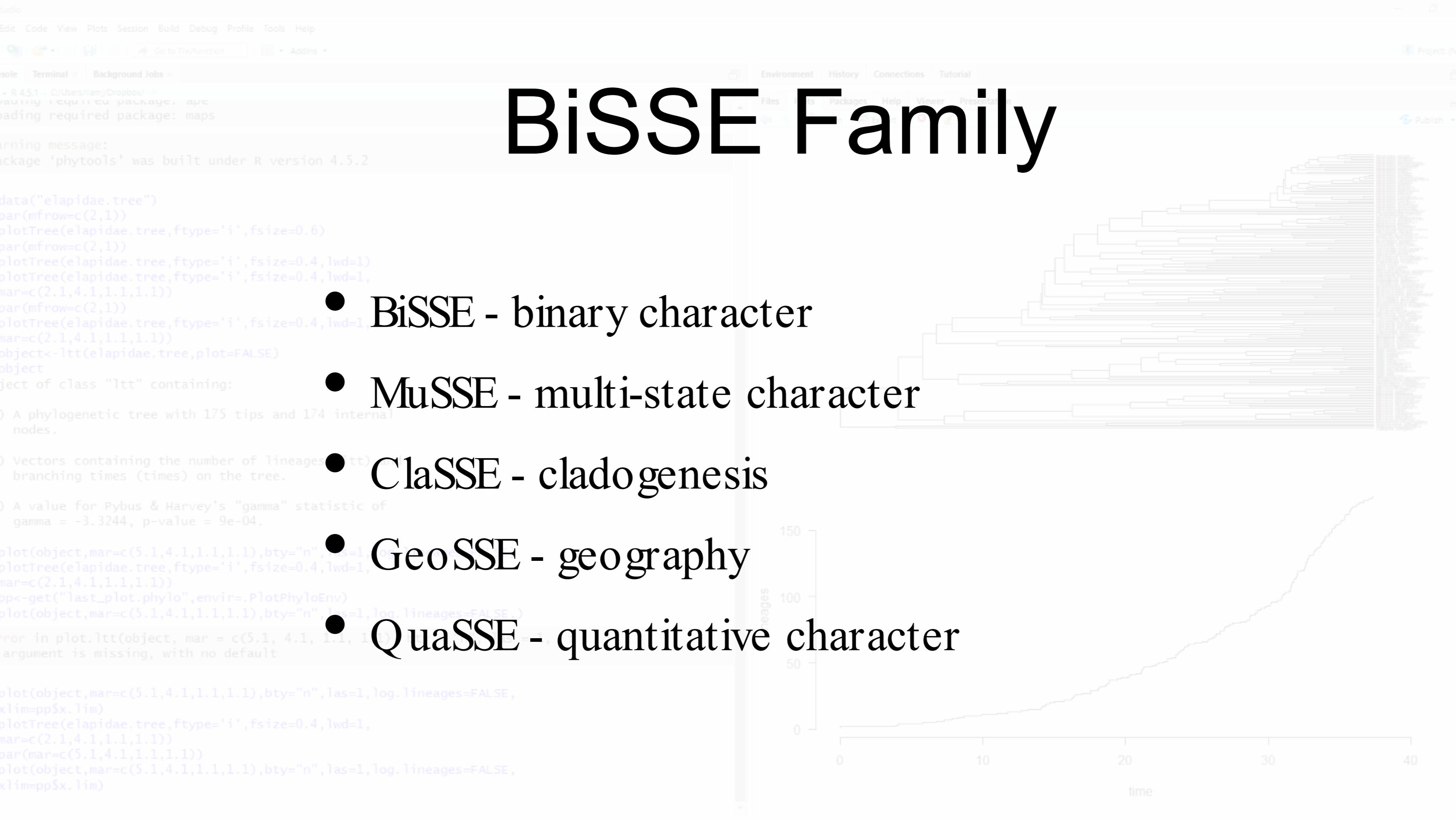
# Trait-dependent diversification models

- We can use BiSSE (and related) models to test for a relationship between traits and diversification rates
- For example, do speciation rates depend on character state?









# BiSSE Family

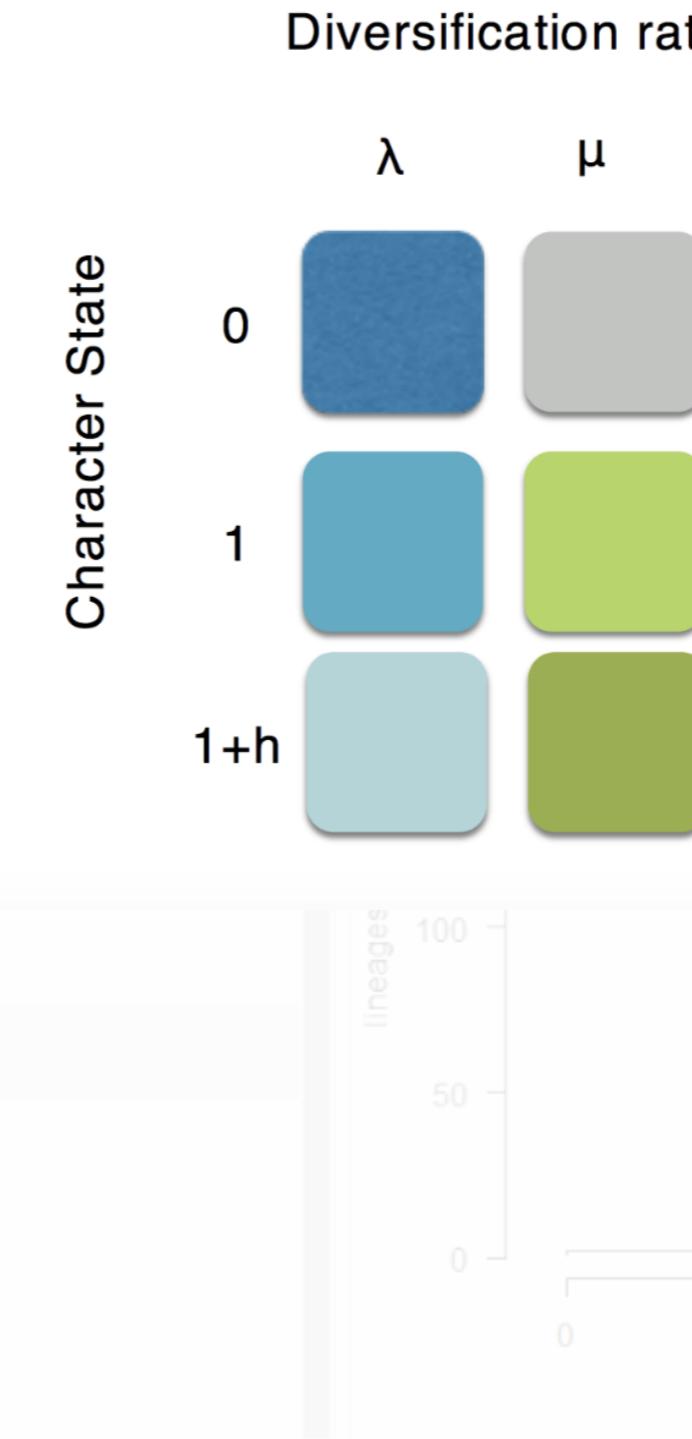
- BiSSE - binary character
- MuSSE - multi-state character
- ClasSE - cladogenesis
- GeoSSE - geography
- QuaSSE - quantitative character





# HiSSE: hidden state speciation and extinction

- HiSSE (hidden state SSE)
- HiSSE allows for null models where diversification rate changes on tree independent of character
- Hidden state also reveals how much your trait model explains relative to all of the trait-related heterogeneity present on the tree







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Go to File/Function Addins

sole Terminal > Background Jobs >

R 4.5.1 - C:/Users/lamj/Dropbox/  
loading required package: ape  
loading required package: maps

Warning message:  
package 'phytools' was built under R version 4.5.2

```
data("elapidae.tree")
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fsize=0.6)
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1)
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1,
mar=c(2.1,4.1,1.1,1.1))
par(mfrow=c(2,1))
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1,
mar=c(2.1,4.1,1.1,1.1))
object<-ltt(elapidae.tree,plot=FALSE)
object
object of class "ltt" containing:
)
A phylogenetic tree with 175 tips and 174 internal nodes.
)
Vectors containing the number of lineages (ltt) and branching times (times).
)
A value for Pybus & Harvey's "gamma" statistic of
gamma = -3.3244, p-value = 9e-04.
```

```
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1,
mar=c(2.1,4.1,1.1,1.1))
op<-get("last_plot.phylo",envir=.PlotPhyloEnv)
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log
error in plot.ltt(object, mar = c(5.1, 4.1, 1.1, 1.1)
argument is missing, with no default
```

```
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log
xlim=pp$xFlim)
plotTree(elapidae.tree,ftype='i',fsize=0.4,lwd=1,
mar=c(2.1,4.1,1.1,1.1))
par(mar=c(5.1,4.1,1.1,1.1))
plot(object,mar=c(5.1,4.1,1.1,1.1),bty="n",las=1,log
xlim=pp$xFlim)
```

