

Macropodoid Modelling

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Getting the Data Together

```
## Warning: package 'RPANDA' was built under R version 3.5.2
## Warning: package 'picante' was built under R version 3.5.2
## Warning: package 'ape' was built under R version 3.5.2
## Warning: package 'vegan' was built under R version 3.5.2
## Warning: package 'permute' was built under R version 3.5.2
## Warning: package 'nlme' was built under R version 3.5.2
## Warning: package 'dplyr' was built under R version 3.5.2
## Warning: package 'geiger' was built under R version 3.5.2
## Warning: package 'phytools' was built under R version 3.5.2
## Warning: package 'mvtnorm' was built under R version 3.5.2
## Warning: package 'ggplot2' was built under R version 3.5.2
```

Now read in the tree files we'll be working with

```
#min.tree <- read.nexus("/Users/Ian/Google.Drive/ANU Herp Work/Macropod_Dating/FossilUncertainty/Macro_
#mean.tree <- read.nexus("/PATH/Macro_MeanAges_CON.tre")
#max.tree <- read.nexus("/PATH/Macro_MaxAges_CON.tre")
#cp.min <- read.nexus("/PATH/Macro_CP_MinAges_CON.tre")
#cp.mean <- read.nexus("/PATH/Macro_CP_EstAges_CON.tre")
#cp.max <- read.nexus("/PATH/Macro_CP_MaxAges_CON.tre")
sampled.trees <- read.tree("/Users/Ian/Google.Drive/ANU Herp Work/Macropod_Dating/REAL_Run5_AllSchemes
empirical.trees <- read.tree("/Users/Ian/Google.Drive/ANU Herp Work/Macropod_Dating/MODEL110_Sampled_Run
```

```
fossil.trees <- read.tree("/Users/Ian/Google.Drive/ANU Herp Work/Macropod_Dating/REAL_Run4_Fossil_51
consensus.tree <- read.nexus("/Users/Ian/Google.Drive/ANU Herp Work/Macropod_Dating/Operators/REAL_Mac
```

Choose the current tree we want to work with

```
tree <- consensus.tree
```

And the hypsodonty data

```
# raw data for all the macropodoid taxa
all.HI <- read.csv("/Users/Ian/Google.Drive/ANU Herp Work/Macropod_Dating/FossilUncertainty/D
# or just species means for the Macropodinae
hypsodonty.index <- read.csv("/Users/Ian/Google.Drive/ANU Herp Work/Macropod_Dating/FossilUncertainty/D
head(hypsodonty.index)
```

```
##           Taxon           HI           HI_Source Diet_Guild
## 1 Baringa_nelsonensis 1.3259480 Couzens & Prideaux 2018 Browser
## 2 Baringa_sp_indet 1.1395682 Couzens & Prideaux 2018 Browser
## 3 Bohra_bandharr 1.0119760 Couzens & Prideaux 2018 <NA>
## 4 Bohra_illumina 0.9373134 Couzens & Prideaux 2018 <NA>
## 5 Bohra_nullarbora 1.0722913 Couzens & Prideaux 2018 <NA>
## 6 Bohra_sp_indet 1.2234637 Couzens & Prideaux 2018 <NA>
## Guild_Source
## 1 Dawson 2006
## 2 Dawson 2006
## 3
## 4
## 5
## 6
```

The C4 plant reconstruction data from Andrae

```
enviro.data <- read.csv("/Users/Ian/Google.Drive/ANU Herp Work/Macropod_Dating/Andrae_S1.csv", header=T
grass.data <- enviro.data[1:25, c(1,3)]
# this will also remove the last sample (from 9.5 mya) which is spurious, and keep just the mean esti
head(enviro.data); head(grass.data)
```

```
## Age Age_Error C4_recon_mean C4_recon_lower C4_recon_upper
## 1 1.0 0.002 59.2 36.7 81.6
## 2 2.0 0.001 36.6 11.8 61.3
## 3 2.5 0.008 36.0 11.2 60.8
## 4 2.8 0.005 35.4 10.5 60.2
## 5 2.8 0.013 21.8 0.0 48.1
## 6 3.0 0.005 38.8 14.3 63.3

## Age C4_recon_mean
## 1 1.0 59.2
## 2 2.0 36.6
## 3 2.5 36.0
## 4 2.8 35.4
## 5 2.8 21.8
## 6 3.0 38.8
```

And the dust flux data from Andrae

```
flux.data <- read.csv("/Users/Ian/Google.Drive/ANU Herp Work/Macropod_Dating/Aeolian_Flux.csv", header=
head(flux.data)
```

```
##           Age A_Flux
```

```
## 1 0.05931646 108.3949
## 2 0.10874684 113.8622
## 3 0.20760760 118.6517
## 4 0.25703797 121.9088
## 5 0.35589873 109.4722
## 6 0.40532911 116.3859
```

As well as the paleotemperature data

```
data(InfTemp)
head(InfTemp)
```

```
##      Age Temperature
## 1 0.000      3.902176
## 2 0.000      2.900296
## 3 0.002      4.309984
## 4 0.002      5.172534
## 5 0.004      3.733446
## 6 0.004      4.309984
```

Trim tree and data down to overlapping taxa

```
# extract the taxa that are in both the tree and
overlaps <- intersect(tree$tip.label, unique(hypsodonty.index$Taxon))
macro.tree <- drop.tip(tree, setdiff(tree$tip.label, overlaps))
#macro.tree <- lapply(tree, drop.tip, tip=tip.drops) # if you're using a set of trees (fossil, sampled)
trim.data <- dplyr::filter(hypsodonty.index, Taxon %in% overlaps)
macro.HI <- trim.data[,2]; names(macro.HI) <- trim.data[,1]; geiger::name.check(macro.tree, macro.HI)
```

```
## [1] "OK"
```

```
macro.HI
```

```
##      Baringa_nelsonensis      Bohra_illuminata
##      1.3259480              0.9373134
##      Dendrolagus_bennettianus      Dendrolagus_dorianus
##      1.0115887              0.9400000
##      Dendrolagus_goodfellowi      Dendrolagus_inustus
##      0.8500000              0.8899909
##      Dendrolagus_lumholtzi      Dendrolagus_matschiei
##      0.9342720              0.9100000
##      Dorcopsis_hageni      Dorcopsis_veterum
##      0.8800000              1.0200000
##      Dorcopsoides_fossilis      Dorcopsulus_vanheurni
##      0.7554314              0.9793040
##      Kurrabi_mahoneyi      Lagorchestes_conspicillatus
##      1.4331210              1.1378107
##      Lagorchestes_hirsutus      Lagostrophus_fasciatus
##      1.2047786              1.1600000
##      Macropus_agilis      Macropus_antilopinus
##      1.1692005              1.2300000
##      Macropus_eugenii      Macropus_fuliginosus
##      1.1109478              1.3630443
##      Macropus_giganteus      Macropus_irma
##      1.3300000              1.1372544
##      Macropus_parma      Macropus_parryi
##      1.3176042              1.3475744
```

```
##           Macropus_pavana           Macropus_robustus
##           1.1823511           1.2418003
## Macropus_rufogriseus           Macropus_rufus
##           1.3500000           1.3978825
## Onychogalea_fraenata           Onychogalea_unguifera
##           1.5000000           1.2694731
## Peradorcas_concinna           Petrogale_assimilis
##           1.2222222           1.1667479
## Petrogale_brachyotis           Petrogale_inornata
##           1.0074257           1.6500000
## Petrogale_lateralis           Petrogale_penicillata
##           1.2076257           1.2858835
## Petrogale_purpureicollis           Petrogale_rothschildi
##           1.8200000           1.4000000
## Petrogale_xanthopus Prionotemnus_palankarinnicus
##           1.2100000           1.0221543
## Proteomodon_anak           Setonix_brachyurus
##           1.0869565           1.0196716
## Thylogale_billardierii           Thylogale_brunii
##           1.1231331           1.0000000
## Thylogale_stigmatica           Thylogale_thetis
##           1.1895715           1.1652379
## Wallabia_bicolor
##           1.1218826
```

If you're working with the raw data, trim tree and data down to just Macropodinae

```
macros <- dplyr::filter(all.HI, Higher_tax == "Macropodinae")
overlaps <- intersect(tree$tip.label, unique(all.HI$Taxon))
trim.tree <- drop.tip(tree, setdiff(tree$tip.label, overlaps))
trim.raw <- filter(macros, Taxon %in% overlaps)
```

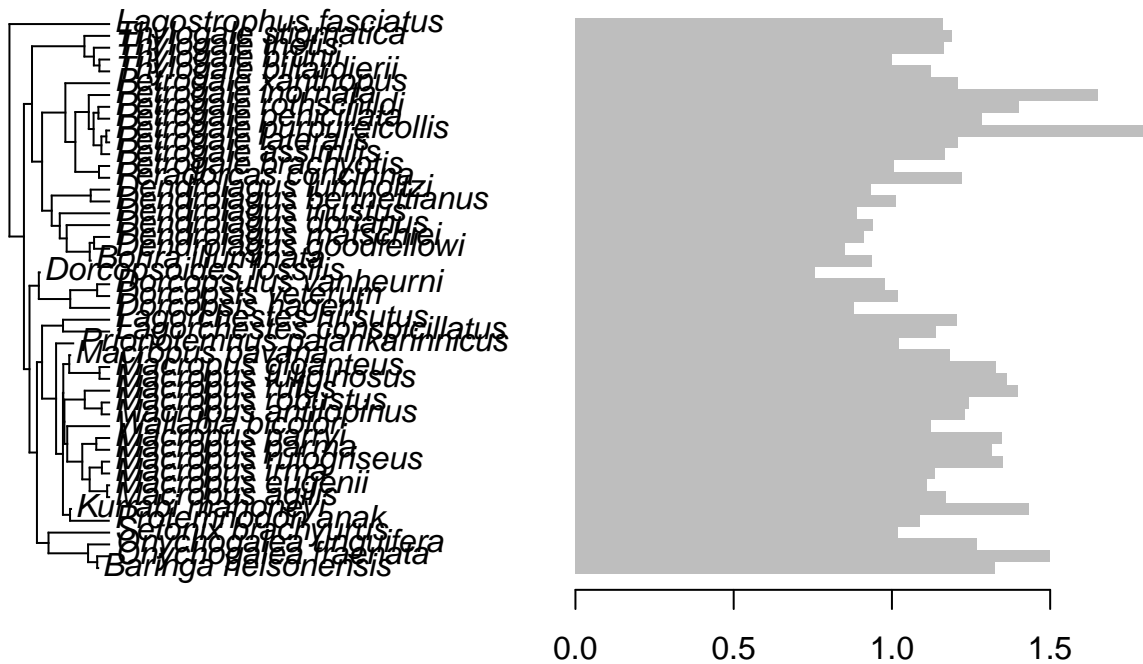
create a tibble to get the species means (if you haven't done this already)

```
library(dplyr)
sp.means <- trim.raw %>%
  group_by(Taxon) %>%
  summarise_at(vars(H_HYPCD/PW), mean)
#write.csv(sp.means, row.names=FALSE, file="/PATH/CrownHeight_Macropodinae_spMEANS.csv") # uncomment
```

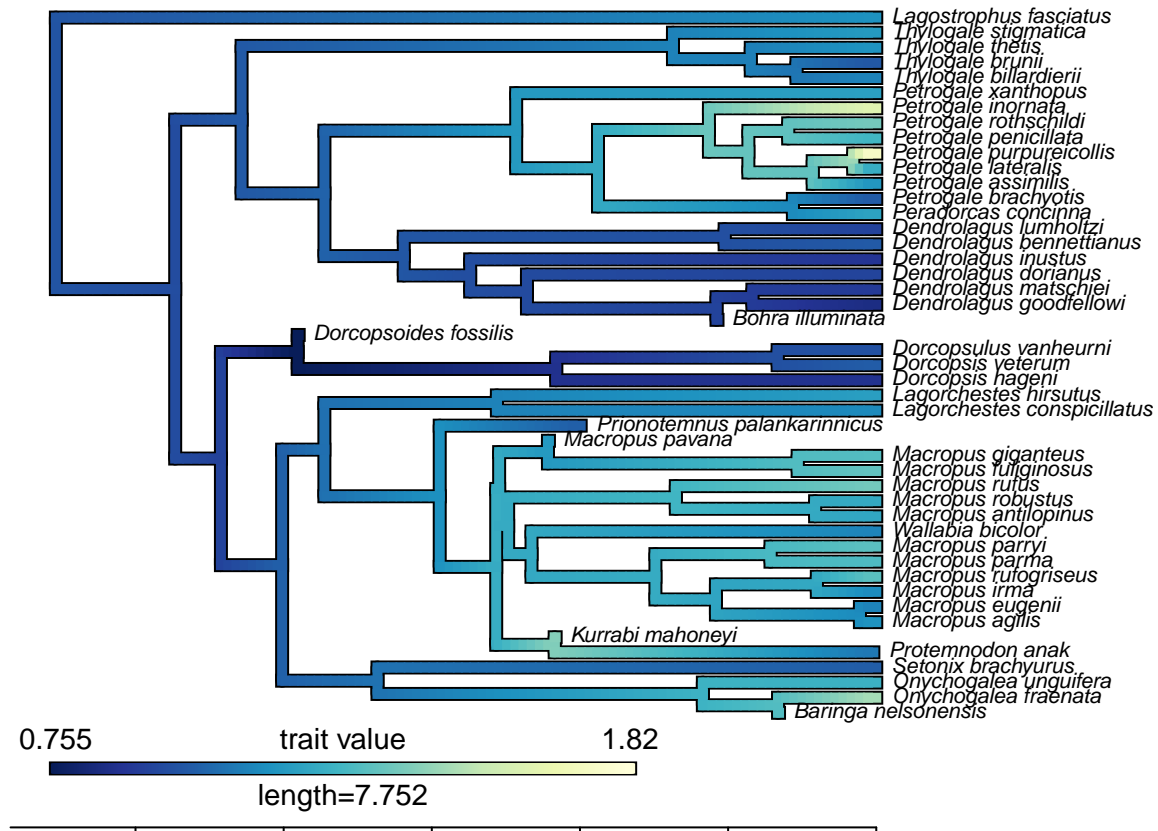
Visualizing Our Data

Let's quickly visualize the data in a few different ways to get an idea of what's going on

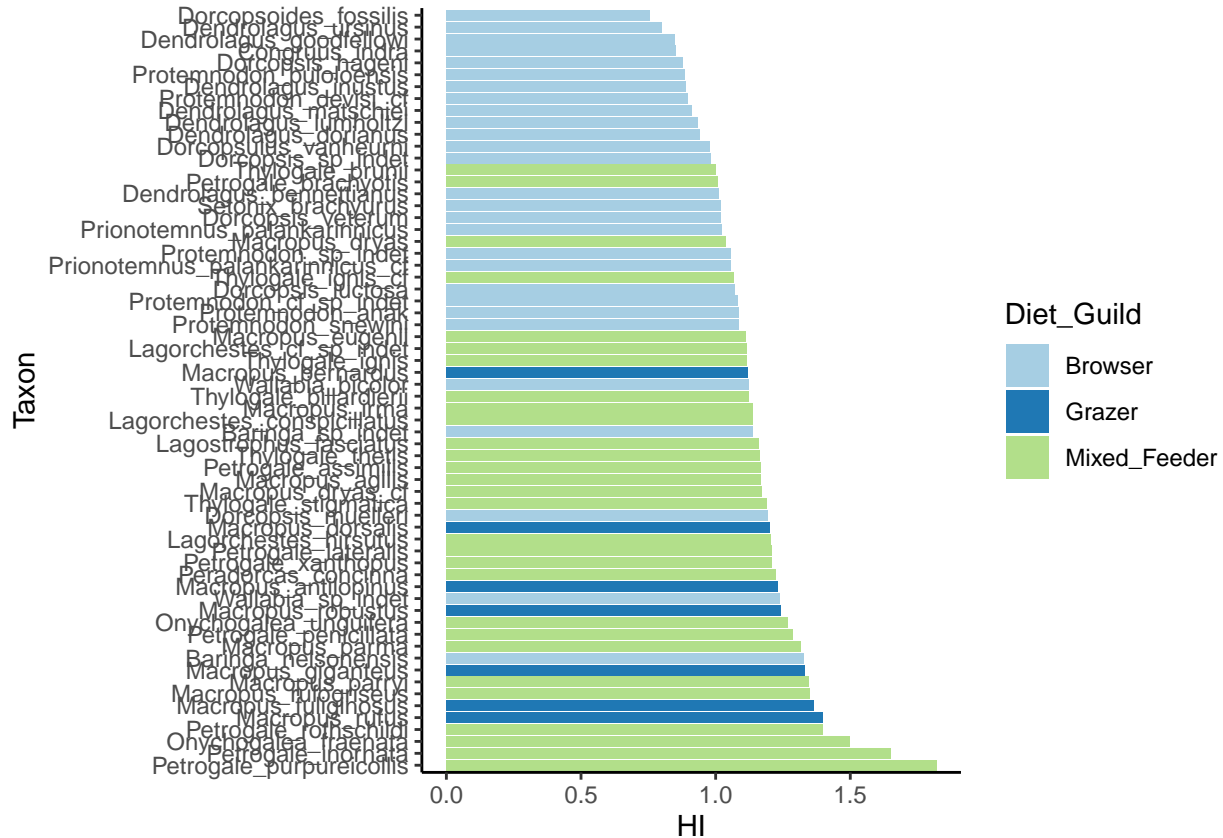
```
# Barplot of trait value
plotTree.barplot(macro.tree, macro.HI, args.barplot=list(beside=TRUE, border=F))
```



```
# Continuous trait map
obj1 <- contMap(macro.tree, macro.HI, plot=FALSE, outline=F);
n<-length(obj1$cols);
obj1$cols[1:n] <- rev(colorRampPalette(brewer.pal(9, "YlGnBu"))(n));
plot(obj1, legend=0.7*max(nodeHeights(obj1$tree)),
     fsize=c(0.7,0.9), lwd=5, border=F); axisPhylo(1, backward=T)
```



```
# Hypsodonty distributed across feeding guilds
hidata <- hypsodonty.index[complete.cases(hypsodonty.index[,c(1,2,4)]),]
hidata <- hidata[order(hidata$HI),]
hidata$Taxon <- factor(hidata$Taxon, levels = hidata$Taxon)
ggplot(hidata, aes(x=Taxon, y=HI, fill=Diet_Guild), colour=brewer.pal(3,"Paired")) +
  geom_col() + theme_classic() + coord_flip() +
  scale_x_discrete(limits = rev(hidata$Taxon)) +
  scale_fill_brewer(palette="Paired", "Diet_Guild")
```

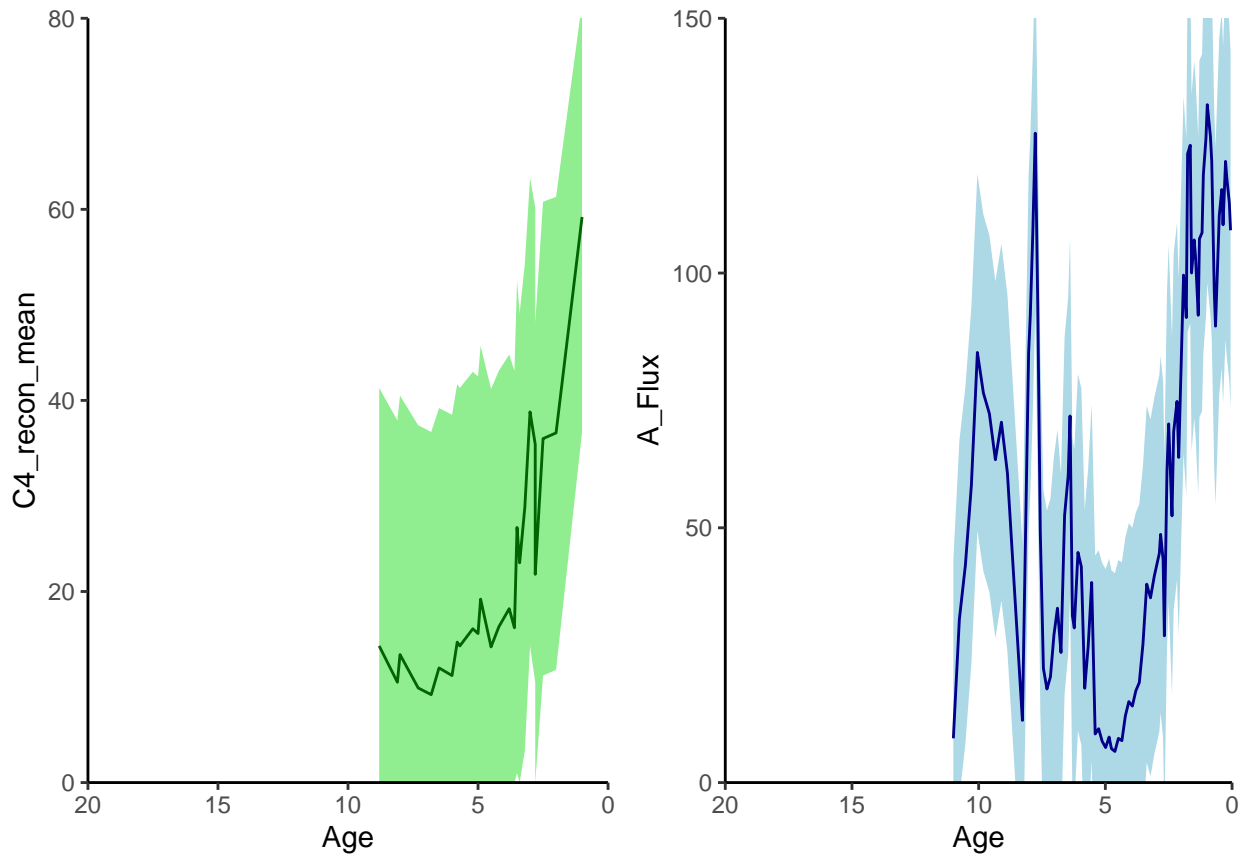


Now we can look at the time-sampled variables

```
# make a plot of the grass data
pp <- ggplot(enviro.data[1:25,], aes(Age)) +
  geom_ribbon(aes(ymin = C4_recon_lower, ymax = C4_recon_upper), fill = "light green") +
  geom_line(aes(y = C4_recon_mean), color="DarkGreen") + scale_x_reverse() + theme_classic() +
  coord_cartesian(xlim = c(0, 20), ylim = c(0,80), expand = FALSE)
#qq <- gggeo_scale(pp, dat="epochs") # if you want to plot a geological timescale

# make a plot of the flux data
rr <- ggplot(flux.data, aes(Age)) +
  geom_ribbon(aes(ymin = A_Flux-35, ymax = A_Flux+35), fill = "light blue") +
  geom_line(aes(y = A_Flux), color="DarkBlue") + scale_x_reverse() + theme_classic() +
  coord_cartesian(xlim = c(0, 20), ylim = c(0,150), expand = FALSE)
#ss <- gggeo_scale(rr, dat="epochs") # if you want to plot a geological timescale

grid.arrange(pp, rr, nrow=1)
```



Fitting Models of Trait Evolution

Correlative models like the environmental models in RPANDA will be sensitive to the amount of smoothing to the trend line of the input data (see Clavel & Morlon, PNAS). To address this, we'll create a function that searches for the optimum smoothness of the trend by fitting a set of values.

```
best.smoothing <- function (phy, trait.data, time.data=InfTemp, degrees=c(0,10,20,30,40,50), model="Env") {
  res.list <- mclapply(1:length(degrees), function(x) {
    fit_t_env(phy, trait.data, env_data=time.data, df=degrees[x], scale=F, plot=T, model=model)}, mc.cores=4)
  for(i in 1:length(res.list)){res.list[[i]]$df <- degrees[i]}
  res.values <- unlist(lapply(res.list, function(x) x$aicc)) # make a vector of the values, so we can get the minimum
  best.res <- res.list[[which.min(res.values)]]

  plot(best.res, main=paste(model, "; AICc = ", round(best.res$aicc,2)), sub=paste("sigma = ",round(best.res$sigma,2)),
        ylab=trait.data, xlab="Age", lty=1, lwd=2, col="black", bty="n", las=1, yaxp=c(1,1,1), xaxp=c(1,1,1))

  return(list(all.results=res.list, best.result=best.res, best.df=best.res$df))
}
```

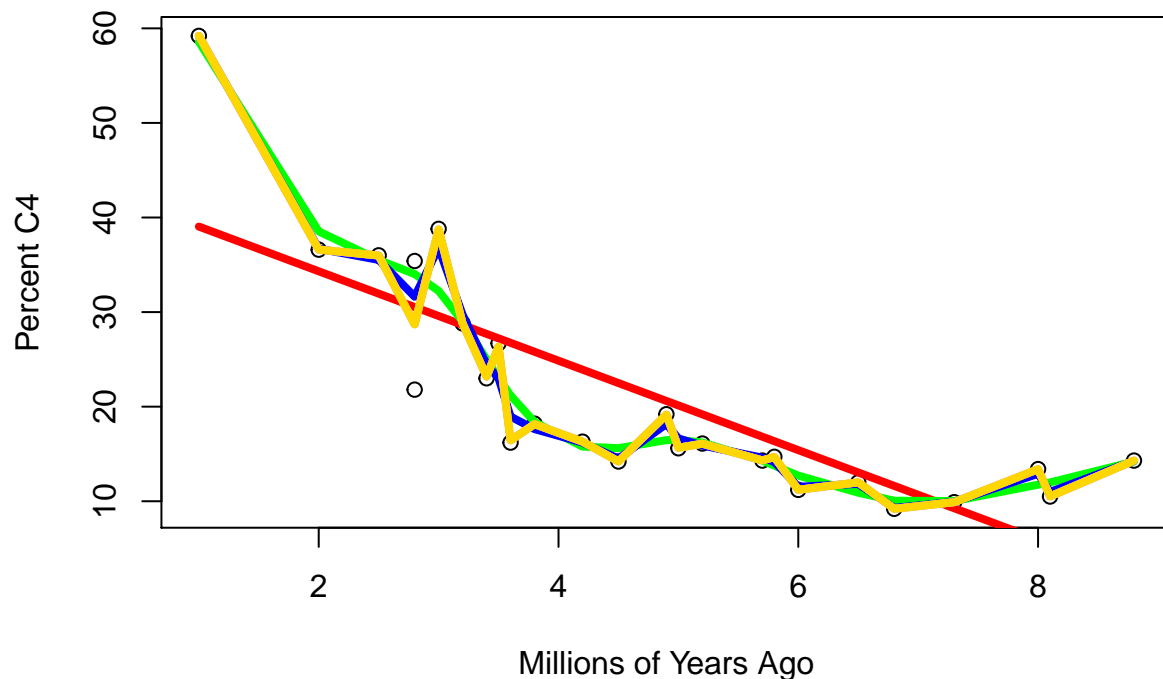
We can have a look at what this smoothing actually does to our data. We can come back to look at these once we get the optimum fits for our models.

```
grass.spline0 <- sm.spline(x=grass.data$Age, y=grass.data$C4_recon_mean, df=0)
grass.spline10 <- sm.spline(x=grass.data$Age, y=grass.data$C4_recon_mean, df=10)
grass.spline20 <- sm.spline(x=grass.data$Age, y=grass.data$C4_recon_mean, df=20)
grass.spline30 <- sm.spline(x=grass.data$Age, y=grass.data$C4_recon_mean, df=30)
grass.spline40 <- sm.spline(x=grass.data$Age, y=grass.data$C4_recon_mean, df=40)
```

```
grass.spline50 <- sm.spline(x=grass.data$Age, y=grass.data$C4_recon_mean, df=50)

plot(grass.data, main="C4 Grass Reconstruction Through Time", xlab="Millions of Years Ago", ylab="Percent C4",
     lines(grass.spline0, col="red", lwd=4)
     lines(grass.spline10, col="green", lwd=4)
     lines(grass.spline20, col="blue", lwd=4)
     lines(grass.spline30, col="yellow", lwd=4)
     lines(grass.spline40, col="violet", lwd=4)
     lines(grass.spline50, col="gold", lwd=4))
```

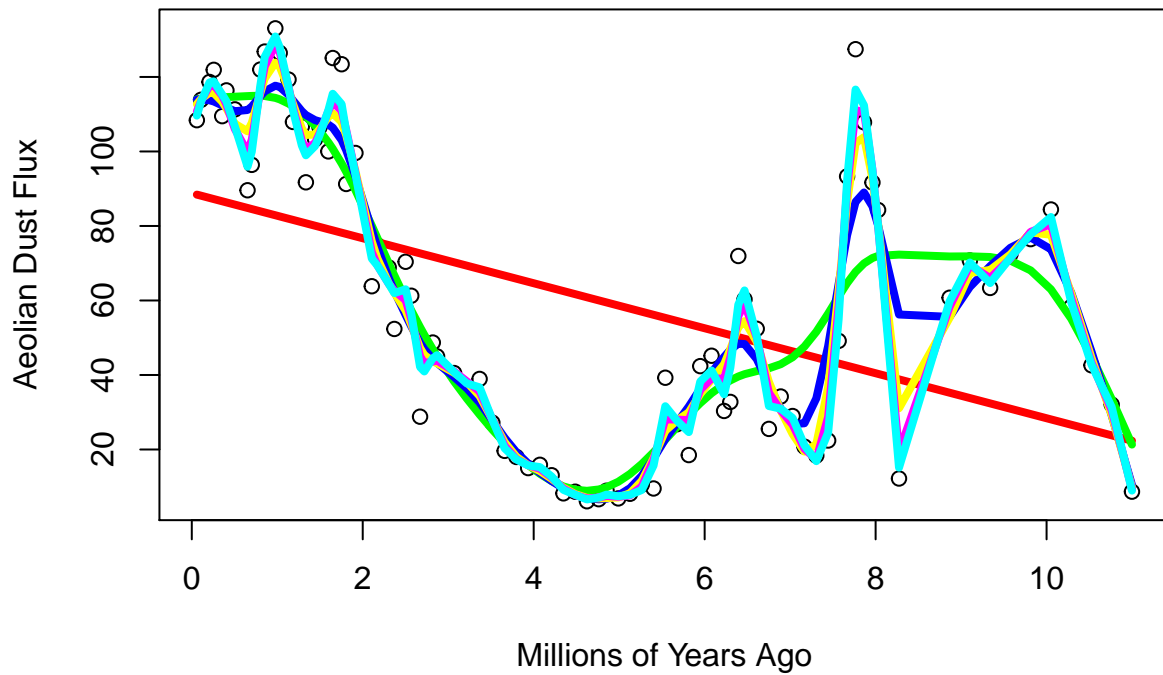
C4 Grass Reconstruction Through Time



```
flux.spline0 <- sm.spline(x=flux.data$Age, y=flux.data$A_Flux, df=0)
flux.spline10 <- sm.spline(x=flux.data$Age, y=flux.data$A_Flux, df=10)
flux.spline20 <- sm.spline(x=flux.data$Age, y=flux.data$A_Flux, df=20)
flux.spline30 <- sm.spline(x=flux.data$Age, y=flux.data$A_Flux, df=30)
flux.spline40 <- sm.spline(x=flux.data$Age, y=flux.data$A_Flux, df=40)
flux.spline50 <- sm.spline(x=flux.data$Age, y=flux.data$A_Flux, df=50)

plot(flux.data, main="Aeolian Dust Flux Through Time", xlab="Millions of Years Ago", ylab="Aeolian Dust",
     lines(flux.spline0, col="red", lwd=4)
     lines(flux.spline10, col="green", lwd=4)
     lines(flux.spline20, col="blue", lwd=4)
     lines(flux.spline30, col="yellow", lwd=4)
     lines(flux.spline40, col="magenta", lwd=4)
     lines(flux.spline50, col="cyan", lwd=4))
```

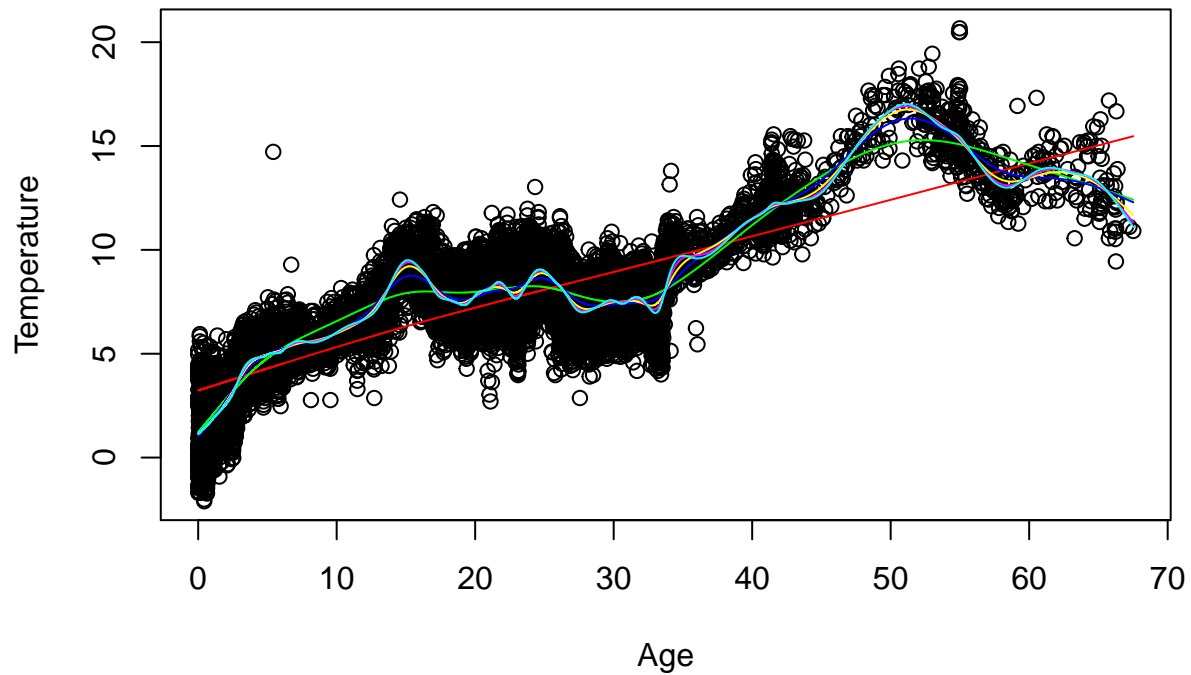

Aeolian Dust Flux Through Time



```
data(InfTemp)
env.spline0 <- sm.spline(x=InfTemp$Age, y=InfTemp$Temperature, df=0)
env.spline10 <- sm.spline(x=InfTemp$Age, y=InfTemp$Temperature, df=10)
env.spline20 <- sm.spline(x=InfTemp$Age, y=InfTemp$Temperature, df=20)
env.spline30 <- sm.spline(x=InfTemp$Age, y=InfTemp$Temperature, df=30)
env.spline40 <- sm.spline(x=InfTemp$Age, y=InfTemp$Temperature, df=40)
env.spline50 <- sm.spline(x=InfTemp$Age, y=InfTemp$Temperature, df=50)

plot(InfTemp, main="Paleotemperature Through Time")
lines(env.spline0, col="red")
lines(env.spline10, col="green")
lines(env.spline20, col="blue")
lines(env.spline30, col="yellow")
lines(env.spline40, col="magenta")
lines(env.spline50, col="cyan")
```

Paleotemperature Through Time

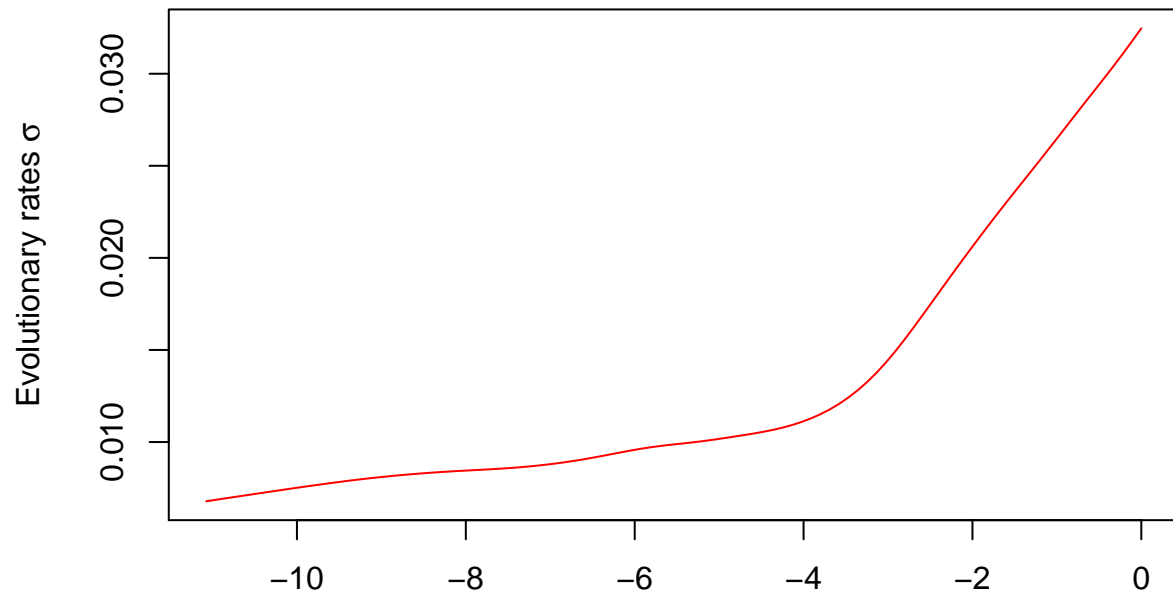


Next we'll fit a number of models to our tree and data

Start with the environmental model of paleotemperature. You can designate the number of cores and the amount of smoothing

```
# linear model first
ENVexp <- best.smoothing(macro.tree, macro.HI, time.data=InfTemp,
                        degrees=c(10,20,30,40,50), model="EnvExp", cores=5)
```

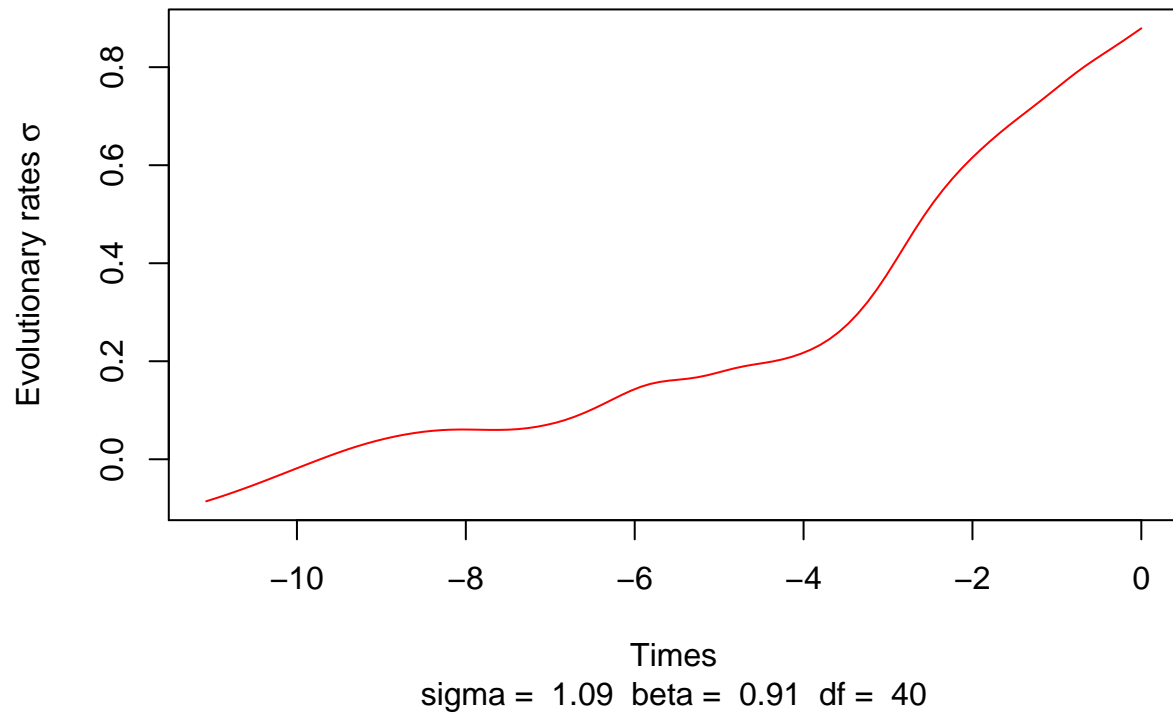
EnvExp ; AICc = 14.21



Times
sigma = 0.05 beta = -0.3 df = 30

```
# exponential model next
ENVlin <- best.smoothing(macro.tree, macro.HI, time.data=InfTemp,
                        degrees=c(10,20,30,40,50), model="EnvLin", cores=5)
```

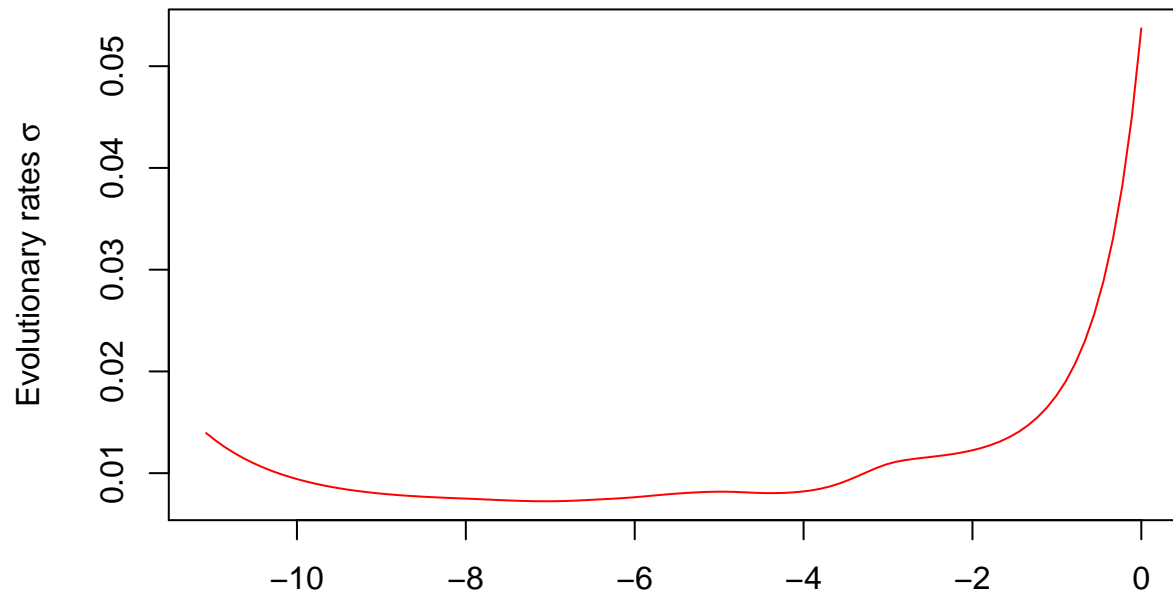
EnvLin ; AICc = 82.08



Next up the grass model, using C4 reconstructions.

```
GRASSexp <- best.smoothing(macro.tree, macro.HI, time.data=grass.data,  
                           degrees=c(10,20,30,40,50), model="EnvExp", cores=5)
```

EnvExp ; AICc = 6.72

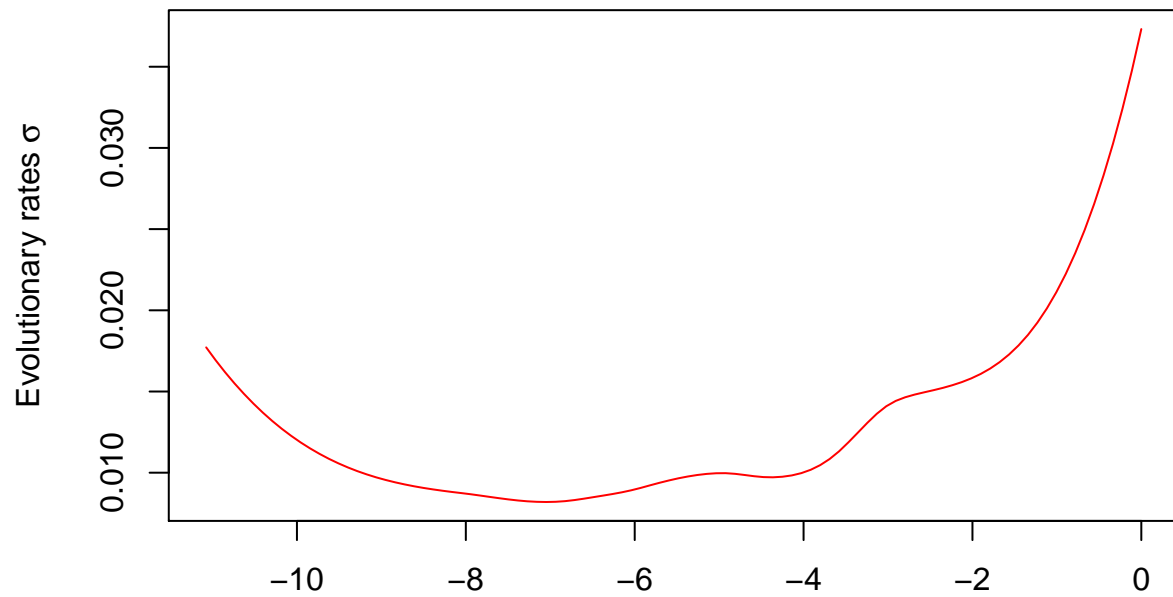


Times

sigma = 0.01 beta = 0.02 df = 10

```
GRASSlin <- best.smoothing(macro.tree, macro.HI, time.data=grass.data,  
degrees=c(10,20,30,40,50), model="EnvLin", cores=5)
```

EnvLin ; AICc = 10.42



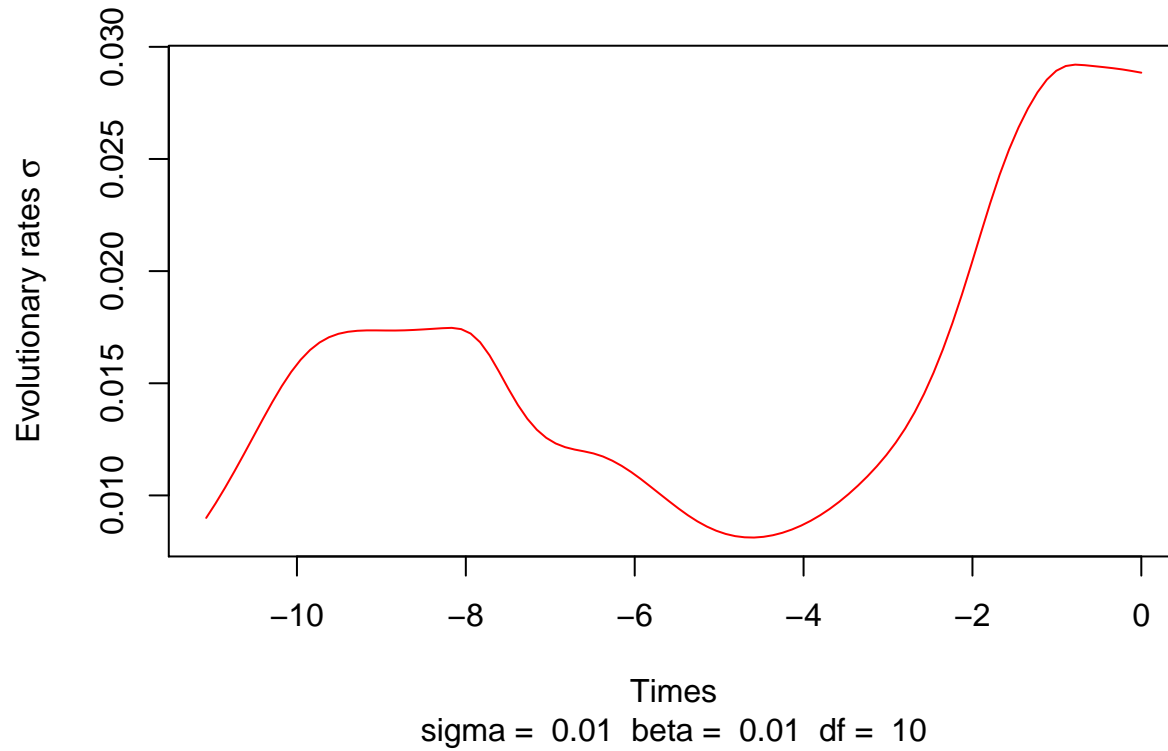
Times

sigma = 0.01 beta = 0.01 df = 10

And finally the flux models, using aeolian dust measurements.

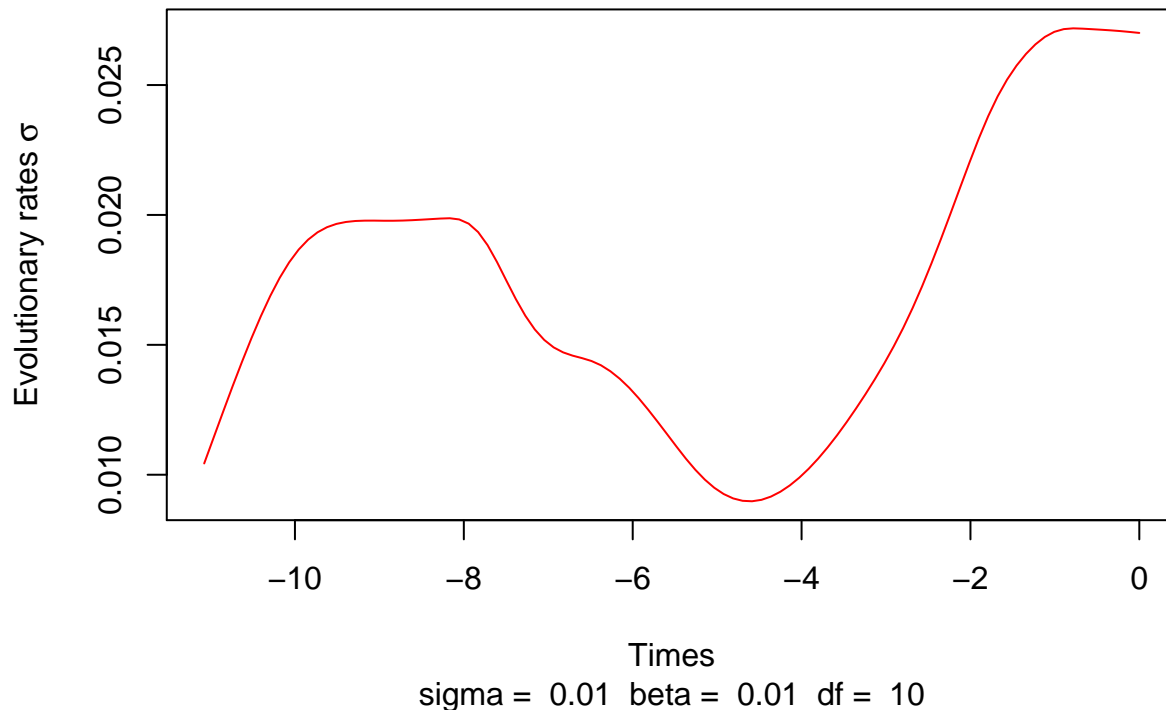
```
FLUXexp <- best.smoothing(macro.tree, macro.HI, time.data=flux.data,  
  degrees=c(10,20,30,40,50), model="EnvExp", cores=5)
```

EnvExp ; AICc = 15.26



```
FLUXlin <- best.smoothing(macro.tree, macro.HI, time.data=flux.data,  
  degrees=c(10,20,30,40,50), model="EnvLin", cores=5)
```

EnvLin ; AICc = 16.34



Lastly, for comparison, run a few standard models. These are Brownian Motion, Brownian Motion with a Trend, and Early Burst.

```
BM_res <- fitContinuous(macro.tree, macro.HI, model="BM")
trend_res <- fitContinuous(macro.tree, macro.HI, model="trend")
EB_res <- fitContinuous(macro.tree, macro.HI, model="EB")
```

```
## Warning in fitContinuous(macro.tree, macro.HI, model = "EB"): Parameter estimates appear at bounds:
## a
```

Compare the models with AICc, and check differences across the trees

```
model_FIT <- c(ENVexp$best.result$aicc, ENVlin$best.result$aicc,
              GRASSlin$best.result$aicc, GRASSexp$best.result$aicc,
              FLUXexp$best.result$aicc, FLUXlin$best.result$aicc,
              BM_res$opt$aicc, trend_res$opt$aicc, EB_res$opt$aicc);
names(model_FIT) <- c("ENVexp", "ENVlin", "GRASSlin", "GRASSexp", "FLUXexp", "FLUXlin", "BM", "Trend", "EB");
aic.w(model_FIT)
```

```
##      ENVexp      ENVlin      GRASSlin      GRASSexp      FLUXexp      FLUXlin
## 0.01949302 0.00000000 0.12961408 0.82510494 0.01154649 0.00672102
##          BM          Trend          EB
## 0.00192663 0.00497934 0.00061449
```

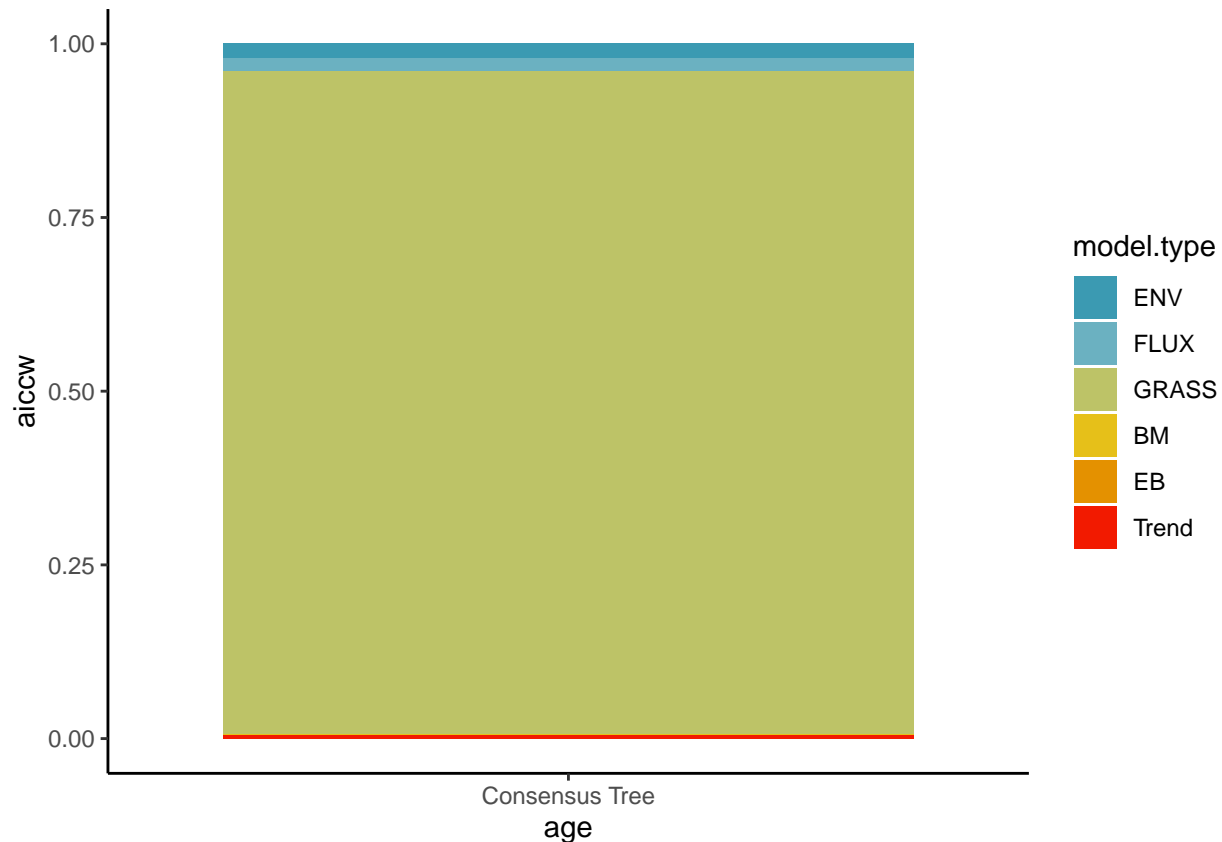
```
fit.aic <- as.data.frame(as.vector(aic.w(model_FIT))); fit.aic$model <- names(model_FIT); colnames(fit.aic) <- c("model", "aic.w")
```

Quickly collapse models from the same data

```
fit.aic$model.type <- c("ENV", "ENV", "GRASS", "GRASS", "FLUX", "FLUX", "BM", "Trend", "EB")
fit.aic$model.type <- factor(fit.aic$model.type, levels=c("ENV", "FLUX", "GRASS", "BM", "EB", "Trend"))
```

Then plot the model fits as AICc weights

```
library(wesanderson)
(ggplot(fit.aic)
+ geom_bar(aes(y=aiccw, x=age, fill=model.type), stat="identity")
# + theme(axis.text.x=element_text(angle=25, hjust=1), panel.background=element_blank(), legend.position="right")
+ theme_classic()
+ scale_fill_manual(values=wes_palette("Zissou1", 6, "continuous")))
```



Fitting Models to Our Data as a Function of Time

Ok, now that we've fit the models to a given tree, we want to fit the models to lots of trees of different ages, shapes, etc. Now we'll run a loop across all of these trees, to fit the models to each one. It may take a little while.

```
# MAKE THIS EVAL=TRUE IF YOU WANT TO DO THIS BIT FOR REAL
tree.span <- fossil.trees
mean.data <- fossil.HI
# Fit all the models to a series of trees!
all.aics <- NULL; all.results <- NULL; timer <- progress_estimated(length(tree.span))
for (k in 1:length(tree.span)){
  int.results <- NULL

  # Fit a number of models to the data (ENV, GRASS, BM, EB, Trend, Drift)
  ENVexp <- best.smoothing(tree.span[[k]], mean.data, time.data=InfTemp,
                           degrees=c(10,20,30,40,50), model="EnvExp", cores=5);
  int.results[["ENVexp"]] <- ENVexp$best.result;
```



```

ENVlin <- best.smoothing(tree.span[[k]], mean.data, time.data=InfTemp,
                        degrees=c(10,20,30,40,50), model="EnvLin", cores=5);
int.results[["ENVlin"]] <- ENVlin$best.result;

GRASSexp <- best.smoothing(tree.span[[k]], mean.data, time.data=grass.data,
                          degrees=c(30,40,50), model="EnvExp", cores=3);
int.results[["GRASSexp"]] <- GRASSexp$best.result;
GRASSlin <- best.smoothing(tree.span[[k]], mean.data, time.data=grass.data,
                          degrees=c(30,40,50), model="EnvLin", cores=3);
int.results[["GRASSlin"]] <- GRASSlin$best.result;

FLUXexp <- best.smoothing(tree.span[[k]], mean.data, time.data=flux.data,
                          degrees=c(10,20,30,40,50), model="EnvExp", cores=5);
int.results[["FLUXexp"]] <- FLUXexp$best.result;
FLUXlin <- best.smoothing(tree.span[[k]], mean.data, time.data=flux.data,
                          degrees=c(10,20,30,40,50), model="EnvLin", cores=5);
int.results[["FLUXlin"]] <- FLUXlin$best.result;

BM_res <- fitContinuous(tree.span[[k]], mean.data, model="BM");
int.results[["BM"]] <- BM_res
trend_res <- fitContinuous(tree.span[[k]], mean.data, model="trend");
int.results[["Trend"]] <- trend_res
EB_res <- fitContinuous(tree.span[[k]], mean.data, model="EB");
int.results[["EB"]] <- EB_res

curr_tree_FIT <- c(ENVexp$best.result$aicc, ENVlin$best.result$aicc,
                  GRASSexp$best.result$aicc, GRASSlin$best.result$aicc,
                  FLUXexp$best.result$aicc, FLUXlin$best.result$aicc,
                  BM_res$opt$aicc, trend_res$opt$aicc, EB_res$opt$aicc);
names(curr_tree_FIT) <- c("ENVexp", "ENVlin", "GRASSexp", "GRASSlin",
                        "FLUXexp", "FLUXlin", "BM", "Trend", "EB")

curr_tree_SIG <- c(ENVexp$best.result$param[[1]], ENVlin$best.result$param[[1]],
                  GRASSexp$best.result$param[[1]], GRASSlin$best.result$param[[1]],
                  FLUXexp$best.result$param[[1]], FLUXlin$best.result$param[[1]],
                  BM_res$opt$sigsq, trend_res$opt$sigsq, EB_res$opt$sigsq);
names(curr_tree_SIG) <- c("ENVexp", "ENVlin", "GRASSexp", "GRASSlin",
                        "FLUXexp", "FLUXlin", "BM", "Trend", "EB")

curr_tree_PAR <- c(ENVexp$best.result$param[[2]], ENVlin$best.result$param[[2]],
                  GRASSexp$best.result$param[[2]], GRASSlin$best.result$param[[2]],
                  FLUXexp$best.result$param[[2]], FLUXlin$best.result$param[[2]],
                  NA, trend_res$opt$slope, EB_res$opt$a);
names(curr_tree_PAR) <- c("ENVexp", "ENVlin", "GRASSexp", "GRASSlin",
                        "FLUXexp", "FLUXlin", "BM", "Trend", "EB")

curr.aic <- as.data.frame(as.vector(aic.w(curr_tree_FIT)));
curr.aic$model <- names(curr_tree_FIT); colnames(curr.aic) <- c("aiccw", "model");
curr.aic$age <- round(max(nodeHeights(tree.span[[k]])), 4)
curr.aic$tree <- k
curr.aic$sigsq <- curr_tree_SIG
curr.aic$par <- curr_tree_PAR
all.results[[k]] <- int.results

```

```

curr.aic$model.type <- c("ENV", "ENV", "GRASS", "GRASS",
                        "FLUX", "FLUX", "BM", "Trend", "EB")

all.aics <- rbind.data.frame(all.aics, curr.aic);

print(timer$tick())
}

```

Save the file externally:

```

saveRDS(all.aics, file="/PATH/Fossil_Trees_Model_Fitting_AICCs.RDS")
saveRDS(all.results, file="/PATH/Fossil_Trees_Model_Fitting_Results.RDS")
#saveRDS(all.aics, file="/PATH/Model_Fitting_AICCs.RDS")

```

Or skip the work and read in the file instead:

```

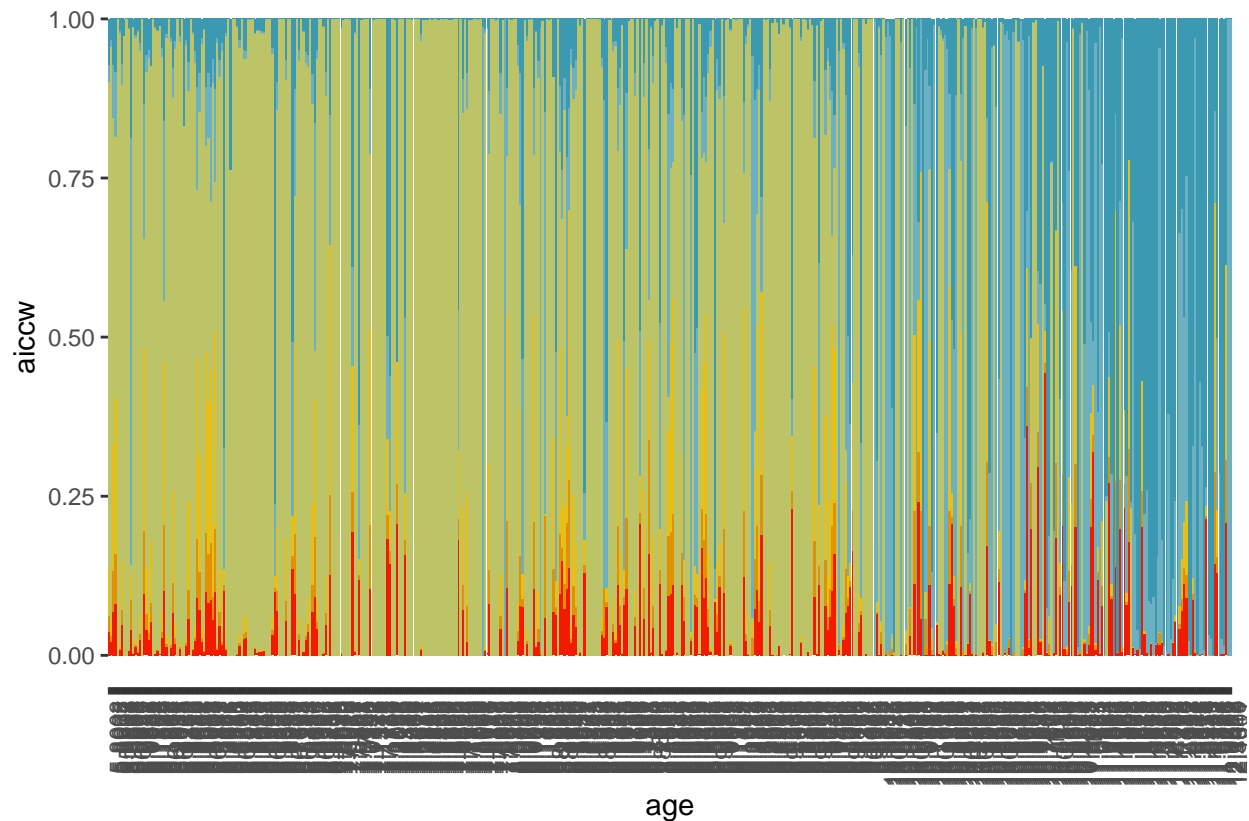
all.aics <- readRDS("/Users/Ian/Google.Drive/ANU Herp Work/Macropod_Dating/FossilUncertainty/Data/FINAL")
all.aics$model.type <- factor(all.aics$model.type, levels=c("ENV", "FLUX", "GRASS", "BM", "EB", "Trend"))
all.aics$age <- as.factor(all.aics$age)

```

```

sampled.res <- (ggplot(all.aics)
+ geom_bar(aes(y=aiccw, x=age, fill=model.type), stat="identity")
+ theme(axis.text.x=element_text(angle=90, hjust=1), panel.background=element_blank(), legend.position="bottom")
+ scale_fill_manual(values=wes_palette("Zissou1", 6, "continuous")))
sampled.res

```



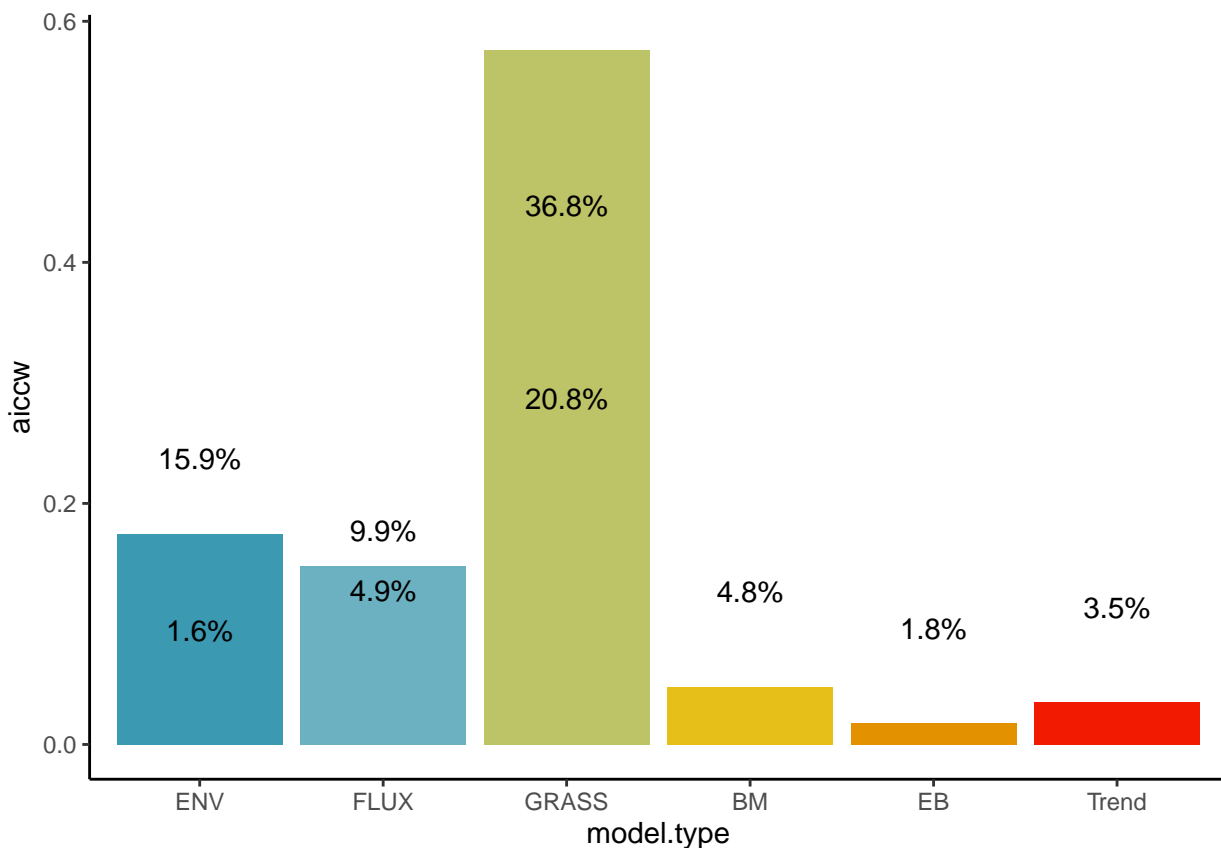
And then summarize the model support (average AICcWt) across all trees

```

# Summarize the model support (average AICcWt)
aic.sum <- summarySE(all.aics, measurevar="aiccw", groupvars="model")
aic.sum$model <- factor(aic.sum$model, levels=c("ENVlin", "ENVexp", "FLUXlin", "FLUXexp", "GRASSexp", "GRASSlin", "Trendlin", "Trendexp", "Trendlin", "Trendexp"))
aic.sum$model.type <- c("BM", "EB", "ENV", "ENV", "FLUX", "FLUX", "GRASS", "GRASS", "Trend")
aic.sum$model.type <- factor(aic.sum$model.type, levels=c("ENV", "FLUX", "GRASS", "BM", "EB", "Trend"))

fossil.bar <- (ggplot(aic.sum, aes(x=model.type, y=aiccw, fill=model.type))
+ geom_bar(stat="identity")
+ geom_errorbar(aes(ymin=aiccw-se, ymax=aiccw+se), size=0.3, width=0.2)
+ scale_fill_manual(values=wes_palette("Zissou1", 6, "continuous"))
+ theme_classic()
+ theme(legend.position="none")
+ facet_wrap(~group, nrow=3, ncol=2)
+ geom_text(aes(label=percent(aiccw), vjust=-4)))
fossil.bar

```



We can also visualize the estimated evolutionary rates of the trait.
First create an adjusted version of the plotting function from RPANDA:

```

# Adjust the RPANDA plotting function so we can fix the axes, and do a bunch of plots
plot.fixed_t_env <- function(x, steps = 100,
                             xlim=c(-10,0), ylim=c(0,1), linecol="red", ...)
{
  if (is.function(x$model)) {
    fun_temp <- function(x, temp, model, param) {
      rate_fun <- function(x) {
        model(x, temp, param)
      }
    }
  }
}

```

```

    }
    rate <- rate_fun(x)
    return(rate)
  }
}
else if (x$model == "EnvExp") {
  fun_temp <- function(x, temp, model, param) {
    sig <- param[1]
    beta <- param[2]
    rate <- (sig * exp(beta * temp(x)))
    return(rate)
  }
}
else if (x$model == "EnvLin") {
  fun_temp <- function(x, temp, model, param) {
    sig <- param[1]
    beta <- param[2]
    rate <- sig + (beta - sig) * temp(x)
    return(rate)
  }
}
t <- seq(0, x$tot_time, length.out = steps)
rates <- fun_temp(x = t, temp = x$env_func, model = x$model,
  param = x$param)
plot(-t, rates, type = "l", xlab = "Times",
  ylab = bquote(paste("Evolutionary rates ",sigma)),
  xlim=xlim, ylim=ylim, col=linecol, ...)
results <- list(time_steps = t, rates = rates)
invisible(results)
}

```

I'll plot just the results from the GRASS-linear model, but you could do this for all.

```

all.aics <- readRDS("/Users/Ian/Google.Drive/ANU Herp Work/Macropod_Dating/FossilUncertainty/Data/FINAL")
all.grass.results <- readRDS("/Users/Ian/Desktop/REAL_SAMPLED_GRASS_Model_Fitting_AllResults.RDS")
sub.aic <- filter(all.aics, model=="GRASSlin" & aiccw > 0.5); sub.trees <- sub.aic$tree; print(paste(ler

```

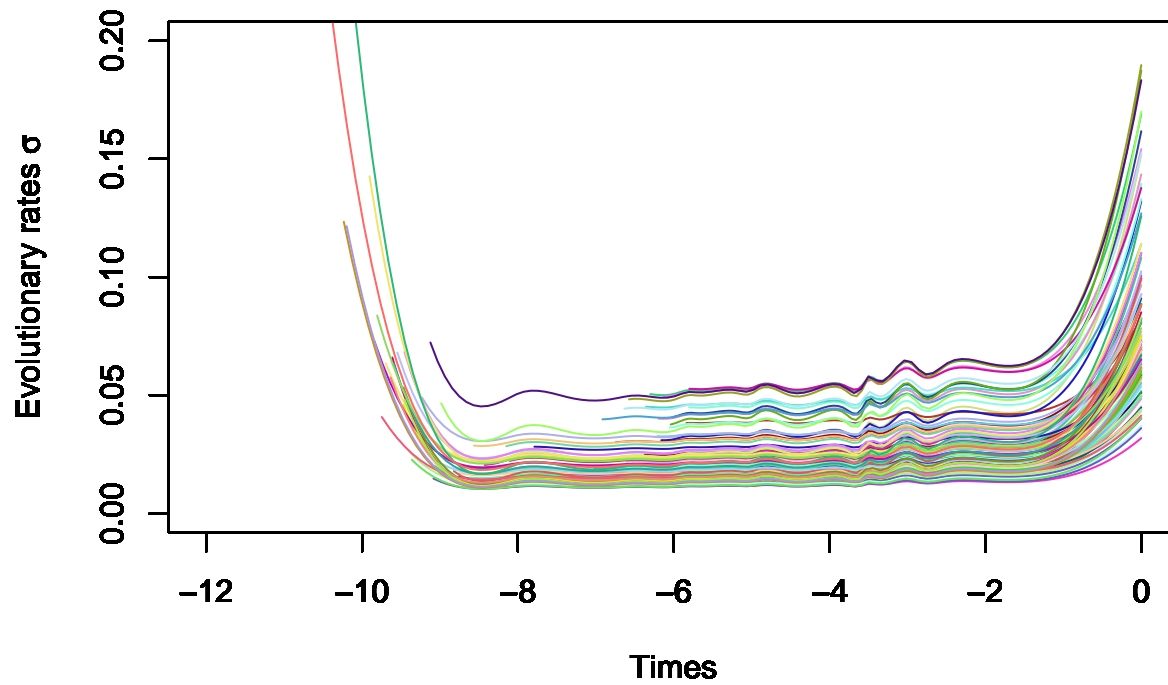
```
## [1] "111 estimates"
```

```

for(i in sub.trees){plot.fixed_t_env(all.grass.results[[i]]$GRASSlin,
  xlim=c(-12,0), ylim=c(0,0.2),
  linecol=randomcoloR::randomColor(1));

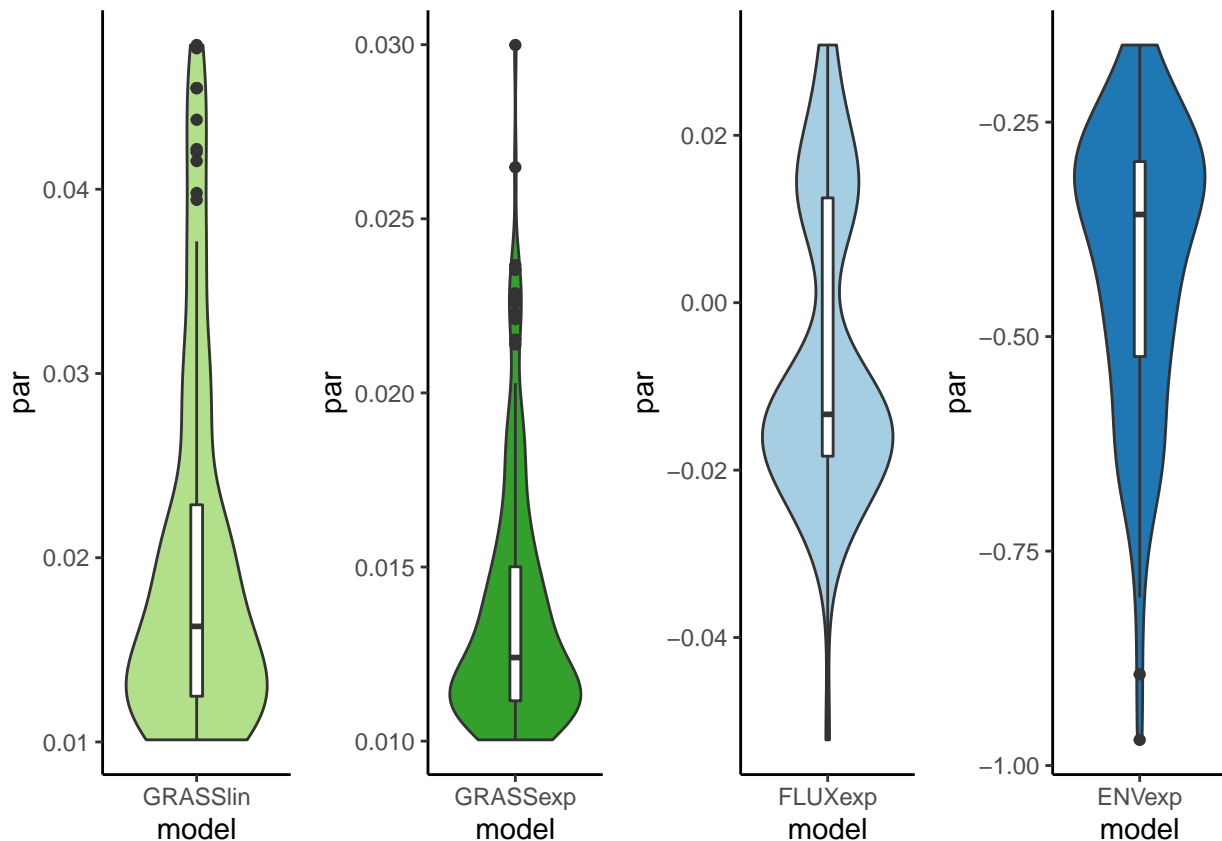
  par(new=T)}

```



Also plot the beta value of the correlation between rate and the variable

```
# And plot the beta values for preferred models
col.pal <- brewer.pal(8, "Paired")
beta.values <- filter(all.aics, model %in% c("GRASSexp", "FLUXexp", "GRASSlin", "ENVexp") & aiccw >= 0.4)
ge_beta <- filter(beta.values, model=="GRASSexp"); ge <- ggplot(ge_beta, aes(x=model, y=par)) + geom_violin()
gl_beta <- filter(beta.values, model=="GRASSlin"); gl <- ggplot(gl_beta, aes(x=model, y=par)) + geom_violin()
fe_beta <- filter(beta.values, model=="FLUXexp"); fe <- ggplot(fe_beta, aes(x=model, y=par)) + geom_violin()
ee_beta <- filter(beta.values, model=="ENVexp"); ee <- ggplot(ee_beta, aes(x=model, y=par)) + geom_violin()
gridExtra::grid.arrange(gl, ge, fe, ee, nrow=1)
```



Comparing Estimated Node Ages Across Dating Schemes

Make a quick function to get the DEPTH of a node (from present), instead of the HEIGHT (from root)

```
MRCA.depth <- function(phy){max(nodeHeights(phy)) - findMRCA(phy, tips=c("Macropus_irma", "Wallabia_bico
```

Prepare trees for comparison of ages

```
# Prepare trees for comparison of ages
max.age.trees <- read.nexus("/Users/Ian/Google.Drive/ANU Herp Work/Macropod_Dating/Operators/REAL_Macro
max.ages <- max.age.trees[sample(1:length(max.age.trees),300)]
#max.ages <- lapply(max.age.trees, drop.tip, tip=setdiff(max.age.trees[[1]]$tip.label, overlaps)); clas
age.max <- as.data.frame(unlist(lapply(max.ages, MRCA.depth)));
age.max$tree <- "fixed.max"; colnames(age.max) <- c("age", "tree")

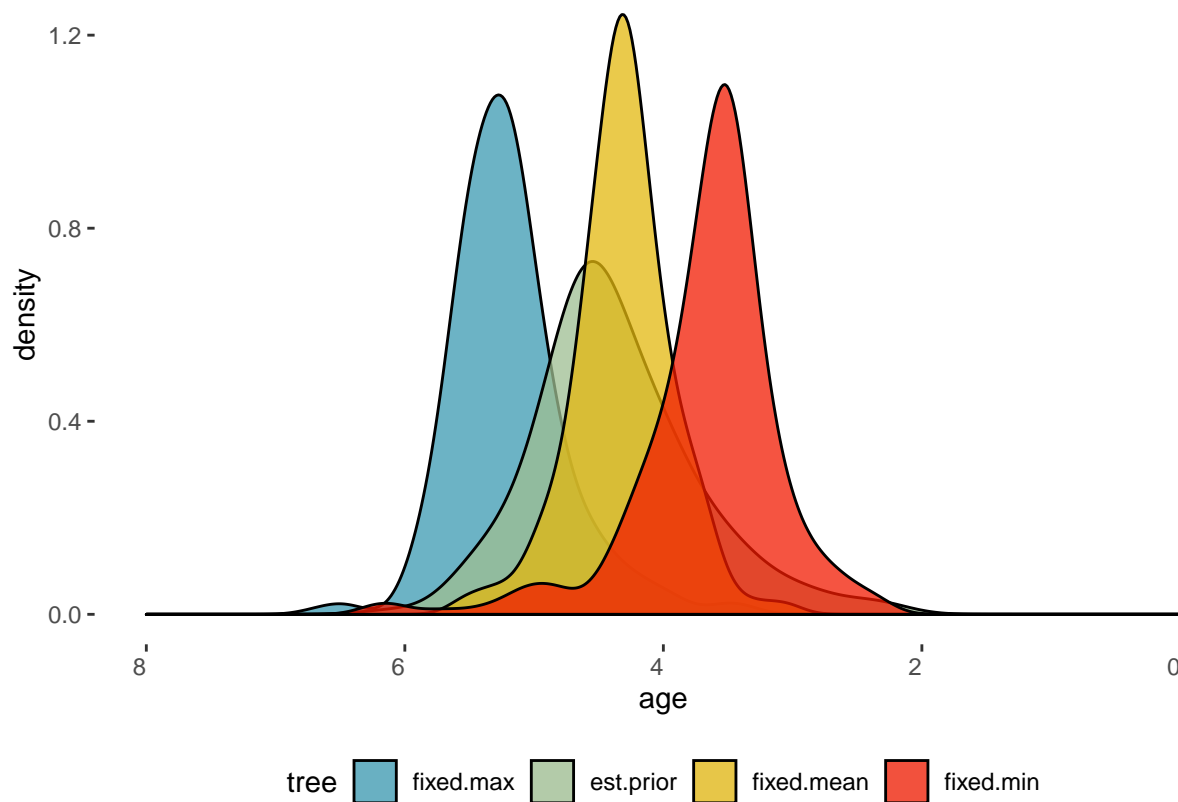
mean.age.trees <- read.nexus("/Users/Ian/Google.Drive/ANU Herp Work/Macropod_Dating/Operators/REAL_Macro
mean.ages <- mean.age.trees[sample(1:length(mean.age.trees),300)]
#mean.ages <- lapply(mean.age.trees, drop.tip, tip=setdiff(mean.age.trees[[1]]$tip.label, overlaps)); c
age.mean <- as.data.frame(unlist(lapply(mean.ages, MRCA.depth)));
age.mean$tree <- "fixed.mean"; colnames(age.mean) <- c("age", "tree")

min.age.trees <- read.nexus("/Users/Ian/Google.Drive/ANU Herp Work/Macropod_Dating/Operators/REAL_Macro
#min.ages <- lapply(min.age.trees, drop.tip, tip=setdiff(min.age.trees[[1]]$tip.label, overlaps)); clas
age.min <- as.data.frame(unlist(lapply(min.ages, MRCA.depth)));
age.min$tree <- "fixed.min"; colnames(age.min) <- c("age", "tree")
```

```
sampld500.trees <- read.nexus("/Users/Ian/Google.Drive/ANU Herp Work/Macropod_Dating/Operators/REAL_Ma
sampld.ages <- sampld500.trees[sample(1:length(sampld500.trees),300)]
sampld500.trees <- read.nexus("/Users/Ian/Google.Drive/ANU Herp Work/Macropod_Dating/Operators/REAL_Ma
sampld.ages <- sampld500.trees[(length(sampld500.trees)-200):length(sampld500.trees)]
#min.ages <- lapply(min.age.trees, drop.tip, tip=setdiff(min.age.trees[[1]]$tip.label, overlaps)); clas
age.sampld <- as.data.frame(unlist(lapply(sampld.ages, MRCA.depth))); age.sampld$tree <- "est.prior"
```

Combine the ages from different dating schemes, and plot them

```
age.all <- rbind(age.min, age.sampld, age.mean, age.max)
age.all$tree <- factor(age.all$tree, levels=c("fixed.max", "est.prior", "fixed.mean", "fixed.min"))
(ggplot(age.all, aes(x=age, fill=tree))
+ geom_density(alpha=0.75, adjust=1.5)
+ theme(axis.text.x=element_text(angle=0, hjust=1), panel.background=element_blank(), legend.position
+ scale_fill_manual(values=wes_palette("Zissou1", type="continuous", 4))
+ scale_x_reverse(lim=c(8,0)))
```



Getting Bayes Factors for Fossil Taxa

Investigating Fossil Taxa as putative Sampled Ancestors or Terminals

```
prior.trees <- read.nexus("/Users/Ian/Google.Drive/ANU Herp Work/Macropod_Dating/Operators/REAL_Macropod
prior.trees <- prior.trees[(length(prior.trees)-1000):length(prior.trees)]
post.trees <- read.nexus("/Users/Ian/Google.Drive/ANU Herp Work/Macropod_Dating/Operators/REAL_Macropod
post.trees <- post.trees[(length(post.trees)-1000):length(post.trees)]
```

Choose which tips you want information for:

```
fossil_taxa <- c("Baringa_nelsonensis", "Congruus_congruus",
               "Kururabi_mahoneyi", "Macropus_pavana")
```

Get the node numbers of the tips

```
nodes <- sapply(fossil_taxa, function(x, y) which(y==x), y=tree$tip.label)
```

Then get the edge lengths for those nodes

```
edge.lengths <- setNames(tree$edge.length[sapply(nodes,
                                                  function(x, y) which(y==x), y=tree$edge[,2])], names(nodes))
```

The faster way is to make a function to do this:

```
get_terminal_branchlengths <- function(phy, tipnames){
  ## Get the node numbers of the tips
  nodes <- sapply(tipnames, function(x, y) which(y==x), y=phy$tip.label)
  ## Then get the edge lengths for those nodes
  edge.lengths <- setNames(phy$edge.length[sapply(nodes,
                                                  function(x, y) which(y==x), y=phy$edge[,2])], names(nodes))
  return(edge.lengths)
}
```

Now that we've got the tips and branch lengths, we can compare the posterior to the prior

```
BFSA <- function(prior.phy, posterior.phy, tips){
  post <- lapply(posterior.phy, get_terminal_branchlengths, tipnames=tips); names(post) <- NULL; post <- NULL; post <- NULL;
  prior <- lapply(prior.phy, get_terminal_branchlengths, tipnames=tips); names(prior) <- NULL; prior <- NULL; prior <- NULL;

  BFs <- NULL
  for (j in 1:length(tips)){
    curr.tip <- subset(post, names(post)==tips[j]);
    probSA <- sum(curr.tip<=0); probTIP <- length(curr.tip)-probSA;

    curr.tip <- subset(prior, names(prior)==tips[j]);
    priorSA <- sum(curr.tip<=0); priorTIP <- length(curr.tip)-priorSA;

    curr.BF <- log((probSA * priorTIP) / (probTIP * priorSA))
    if(is.na(curr.BF)){curr.BF <- 0}

    #curr.BF <- log(probSA/(length(curr.tip)-probSA))
    names(curr.BF) <- tips[j]; curr.BF <- round(curr.BF, 2)
    BFs <- append(BFs, curr.BF)
  }
  return(BFs)
}
```

Orient the data appropriately

```
macro_BFs <- BFSA(prior.trees, post.trees, tips=fossil_taxa)
```

```
macro_BFs <- as.data.frame(macro_BFs) # make the vector a data frame
macro_BFs[which(macro_BFs$macro_BFs > 5),] <- 5 # change any really big (INF) numbers to 5
macro_BFs[which(macro_BFs$macro_BFs < -5),] <- -5 # change any really small (-INF) numbers to -5
```

```
macro_BFs$taxa <- rownames(macro_BFs); # create column with the taxon names
macro_BFs <- macro_BFs[order(macro_BFs$macro_BFs),] # reorder by BF values
```



```

# set colors for plotting
macro_BFs$color <- "black";
#macro_BFs[which(macro_BFs$macro_BFs > 1),]$color <- "#3d98d3"
macro_BFs[which(macro_BFs$macro_BFs < -1),]$color <- "#FF7175"

macro_BFs$taxa <- factor(macro_BFs$taxa, levels=c(macro_BFs$taxa)) # set factors for plotting (NOT NEEDED)

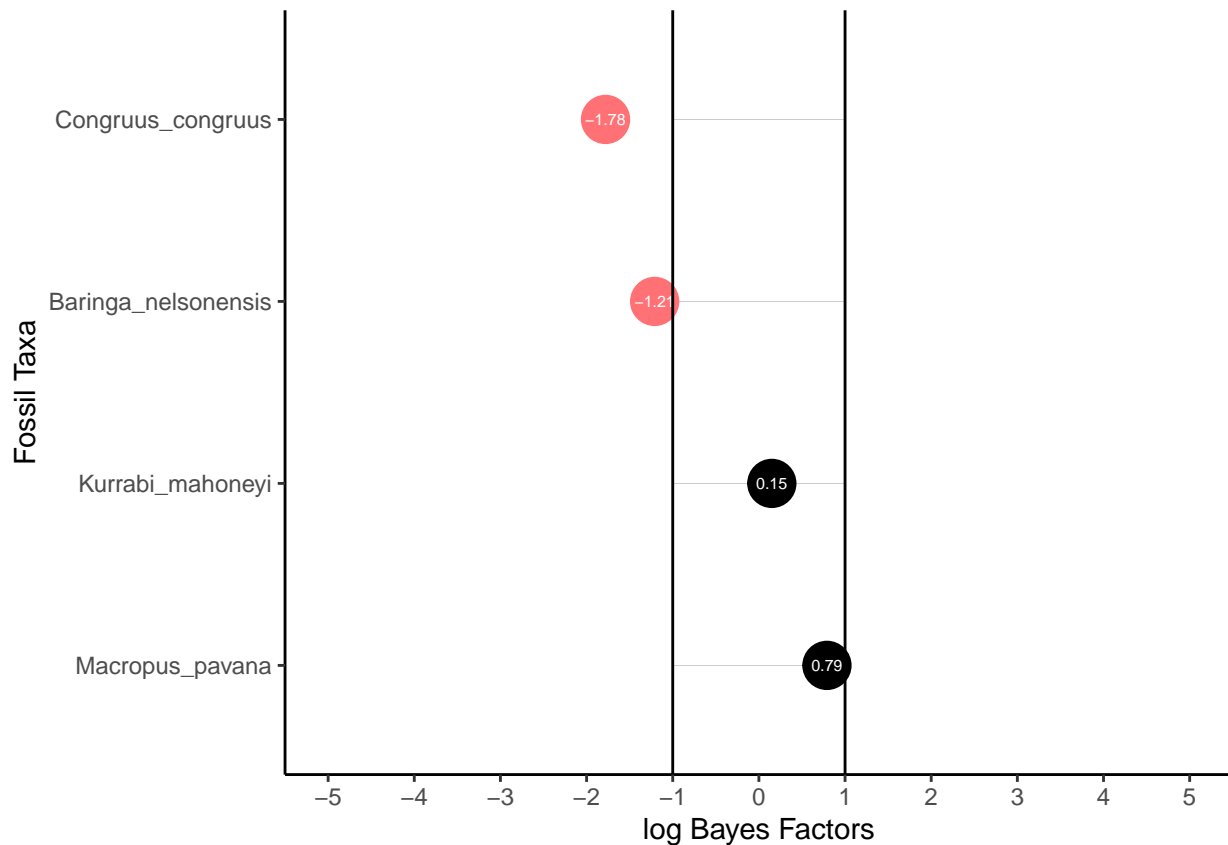
```

Then plot the data

```

ggplot(macro_BFs, aes(x=taxa, y=macro_BFs, label=macro_BFs)) +
  geom_ribbon(aes(ymin=-1, ymax=+1)) +
  geom_point(stat='identity', size=8, color=macro_BFs$color) +
  # geom_segment(aes(y = 0,
  #                   x = taxa,
  #                   yend = macro_BFs,
  #                   xend = taxa),
  #              color = macro_BFs$color) +
  geom_text(color="white", size=2) +
  #labs(title="Bayes Factor Support", subtitle="for Fossil Taxa as Sampled Ancestors") +
  #ylim(-5, 5) +
  scale_y_continuous(name="log Bayes Factors", limits=c(-5,5), breaks=c(-5:5)) +
  scale_x_discrete(limits = rev(unique(sort(macro_BFs$taxa)))) + # drop this if you want to order it differently
  #theme(panel.background=element_blank()) +
  geom_hline(yintercept=-1) +
  geom_hline(yintercept=1) +
  xlab("Fossil Taxa") +
  #ylab("log Bayes Factors") +
  theme_classic() +
  #theme(axis.text.y=element_blank(), axis.title.y=element_blank()) +
  coord_flip()

```



Investigating estimated ages of fossils

Create a function to pull the ages of each fossil taxon estimated

```
get.fossil.ages <- function(fossil.tips, trees){
  tree.tables <- lapply(trees, print.tree)
  fossil.tables <- lapply(1:length(tree.tables), function(x) {
    subset(tree.tables[[x]], tree.tables[[x]]$label %in% fossil.tips)
  })
  fossil.ages <- lapply(1:length(fossil.tables), function(x) {
    select(fossil.tables[[x]], label, time_bp)
  })
  final <- bind_rows(fossil.ages)
}
```

Need to create a function called “print.tree” that I borrowed some code from biogeoBEARS

Now pull out the info on those fossils

```
my.test <- get.fossil.ages(fossil.tips = fossil_taxa, trees = post.trees)

(ggplot(my.test, aes(x=time_bp, y=label, fill=..x..))
 + scale_fill_gradientn(colours=wes_palette("Zissou1"))
 + geom_density_ridges_gradient(scale=1.5)
 + scale_x_reverse()
 + theme_classic())
```

Picking joint bandwidth of 0.6

