‘SongEvo’ package

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Introduction

SongEvo simulates the cultural evolution of quantitative traits of bird song. SongEvo is an individual- (agent-) based model. SongEvo is spatially-explicit and can be parameterized with, and tested against, measured song data. Functions are available for model implementation, sensitivity analyses, parameter optimization, model validation, and hypothesis testing.

Overview of Functions

1. `SongEvo` implements the model
2. `par.sens` allows sensitivity analyses
3. `par.opt` allows parameter optimization
4. `mod.val` allows model validation
5. `h.test` allows hypothesis testing

Getting Started

Load and attach SongEvo package

```r
library(SongEvo)
```

Functions

`SongEvo` implements the model `par.sens` allows sensitivity analyses `par.opt` allows parameter optimization `mod.val` allows model validation `h.test` allows hypothesis testing

Examples

EXAMPLE 1

Load the example data: song.data and global parameters

To explore the SongEvo package, we will use a database of songs from Nuttall’s white-crowned sparrow (*Zonotrichia leucophrys nuttalli*) recorded at three locations in 1969 and 2005.

```r
data("song.data")
```

Examine global parameters. Global parameters describe our understanding of the system and may be measured or hypothesized. They are called “global” because they are used by many many functions and subroutines within functions. For descriptions of all adjustable parameters, see `?song.data`.

```
data("glo.parms")
str(glo.parms)
#> List of 15
#>  $ learning.error.d  : num 0
#>  $ learning.error.sd : num 430
#>  $ n.territories     : num 40
#>  $ mortality.a       : num 0.468
#>  $ mortality.j       : num 0.5
#>  $ lifespan          : num 2.08
#>  $ phys.lim.min      : num 1559
#>  $ phys.lim.max      : num 4364
#>  $ male.fledge.n.mean: num 1.35
#>  $ male.fledge.n.sd  : num 0.5
#>  $ disp.age          : num 2
#>  $ disp.distance.mean: num 110
#>  $ disp.distance.sd  : num 100
#>  $ terr.turnover     : num 0.5
#>  $ male.fledge.n     : num [1:40] 1 1 2 1 0 2 2 2 2 1 ...
```

Share global parameters with the global environment. We make these parameters available in the global environment so that we can access them with minimal code.

```
list2env(glo.parms, globalenv())
#> <environment: R_GlobalEnv>
```

Examine song data

Data include the population name (Bear Valley, PRBO, or Schooner), year of song recording (1969 or 2005), and the frequency bandwidth of the trill.

```
str(song.data)
#> 'data.frame':    89 obs. of  3 variables:
#>  $ Population: Factor w/ 3 levels "Bear Valley",..: 3 3 3 3 3 3 3 3 3 3 ...
#>  $ Year      : int  1969 1969 1969 1969 1969 1969 1969 1969 1969 1969 ...
#>  $ Trill.FBW : num  3261 2494 2806 2878 2758 ...
```

Simulate bird song evolution with `SongEvo()`

Define initial individuals

In this example, we use songs from individual birds recorded in one population (PRBO) in the year 1969, which we will call `starting.trait`.

```
starting.trait <- subset(song.data, Population=="PRBO" & Year==1969)$Trill.FBW
```

We want a starting population of 40 individuals, so we generate additional trait values to complement those from the existing 30 individuals. Then we create a data frame that includes a row for each individual; we add identification numbers, ages, and geographical coordinates for each individual.

```
starting.trait2 <- c(starting.trait, rnorm(n.territories-length(starting.trait),
    mean=mean(starting.trait), sd=sd(starting.trait)))
init.inds <- data.frame(id = seq(1:n.territories), age = 2, trait = starting.trait2)
init.inds$x1 <-  round(runif(n.territories, min=-122.481858, max=-122.447270), digits=8)
init.inds$y1 <-  round(runif(n.territories, min=37.787768, max=37.805645), digits=8)
```

Specify and call the SongEvo model

`SongEvo()` includes several settings, which we specify before running the model. For this example, we run the model for 10 iterations, over 36 years (i.e. 1969–2005). When conducting research with `SongEvo()`, users will want to increase the number iterations (e.g. to 100 or 1000). Each timestep is one year in this model (i.e. individuals complete all components of the model in 1 year). We specify territory turnover rate here as an example of how to adjust parameter values. We could adjust any other parameter value here also. The learning method specifies that individuals integrate songs heard from adults within the specified integration distance (intigrate.dist, in kilometers). In this example, we do not includ a lifespan, so we assign it NA. In this example, we do not model competition for mates, so specify it as FALSE. Last, specify all as TRUE in order to save data for every single simulated individual because we will use those data later for mapping. If we do not need data for each individual, we set all to FALSE because the all.inds data.frame becomes very large!

```
iteration <- 10
years <- 36
timestep <- 1
terr.turnover <- 0.5
learning.method <- "integrate"
integrate.dist <- 0.1
lifespan <- NA
mate.comp <- FALSE
prin <- FALSE
all <- TRUE
```

Now we call SongEvo with our specifications and save it in an object called SongEvo1.

```
SongEvo1 <- SongEvo(init.inds = init.inds, iteration = iteration, steps = years,
    timestep = timestep, n.territories = n.territories, terr.turnover = terr.turnover,
    learning.method = learning.method, integrate.dist = integrate.dist,
    learning.error.d = learning.error.d, learning.error.sd = learning.error.sd,
    mortality.a = mortality.a, mortality.j = mortality.j, lifespan = lifespan,
    phys.lim.min = phys.lim.min, phys.lim.max = phys.lim.max,
    male.fledge.n.mean = male.fledge.n.mean, male.fledge.n.sd = male.fledge.n.sd,
    male.fledge.n = male.fledge.n, disp.age = disp.age,
    disp.distance.mean = disp.distance.mean, disp.distance.sd = disp.distance.sd,
    mate.comp = mate.comp, prin = prin, all)
```

Examine results from SongEvo model

The model required the following time to run on your computer:

```
SongEvo1$time
#>    user  system elapsed
#>   2.028   0.038   2.067
```

Three main objects hold data regarding the SongEvo model. Additional objects are used temporarily within modules of the model.

First, currently alive individuals are stored in a data frame called “inds.” Values within “inds” are updated throughout each of the iterations of the model, and “inds” can be viewed after the model is completed.

```
head(SongEvo1$inds, 5)
#>                  coordinates   id age    trait        x1       y1
#> 1639  (-122.4451, 37.7949) 1639   7 4254.498 -122.4451 37.79490
#> 1667 (-122.4569, 37.79478) 1667   7 3926.433 -122.4569 37.79478
#> 1673 (-122.4786, 37.79496) 1673   6 3614.355 -122.4786 37.79496
#> 1677 (-122.4444, 37.79398) 1677   6 3980.020 -122.4444 37.79398
#> 1687 (-122.4789, 37.79058) 1687   6 3225.836 -122.4789 37.79058
#>      male.fledglings territory father        x0       y0
#> 1639               2         1   1552 -122.4452 37.79496
#> 1667               1         1   1614 -122.4586 37.79547
#> 1673               1         1   1487 -122.4765 37.79480
#> 1677               0         0   1552 -122.4452 37.79496
#> 1687               0         0   1590 -122.4793 37.78913
```

Second, an array (i.e. a multi-dimensional table) entitled "summary.results" includes population summary values for each time step (dimension 1) in each iteration (dimension 2) of the model. Population summary values are contained in five additional dimensions: population size for each time step of each iteration ("sample.n"), the population mean and variance of the song feature studied ("trait.pop.mean" and "trait.pop.variance"), with associated lower ("lci") and upper ("uci") confidence intervals.

```
dimnames(SongEvo1$summary.results)
#> $iteration
#>  [1] "iteration 1"  "iteration 2"  "iteration 3"  "iteration 4"
#>  [5] "iteration 5"  "iteration 6"  "iteration 7"  "iteration 8"
#>  [9] "iteration 9"  "iteration 10"
#>
#> $step
#>  [1] "1"  "2"  "3"  "4"  "5"  "6"  "7"  "8"  "9"  "10" "11" "12" "13" "14"
#> [15] "15" "16" "17" "18" "19" "20" "21" "22" "23" "24" "25" "26" "27" "28"
#> [29] "29" "30" "31" "32" "33" "34" "35" "36"
#>
#> $feature
#> [1] "sample.n"           "trait.pop.mean"     "trait.pop.variance"
#> [4] "lci"                "uci"
```

Third, individual values may optionally be concatenated and saved to one data frame entitled "all.inds." all.inds can become quite large, and is therefore only recommended if additional data analyses are desired.

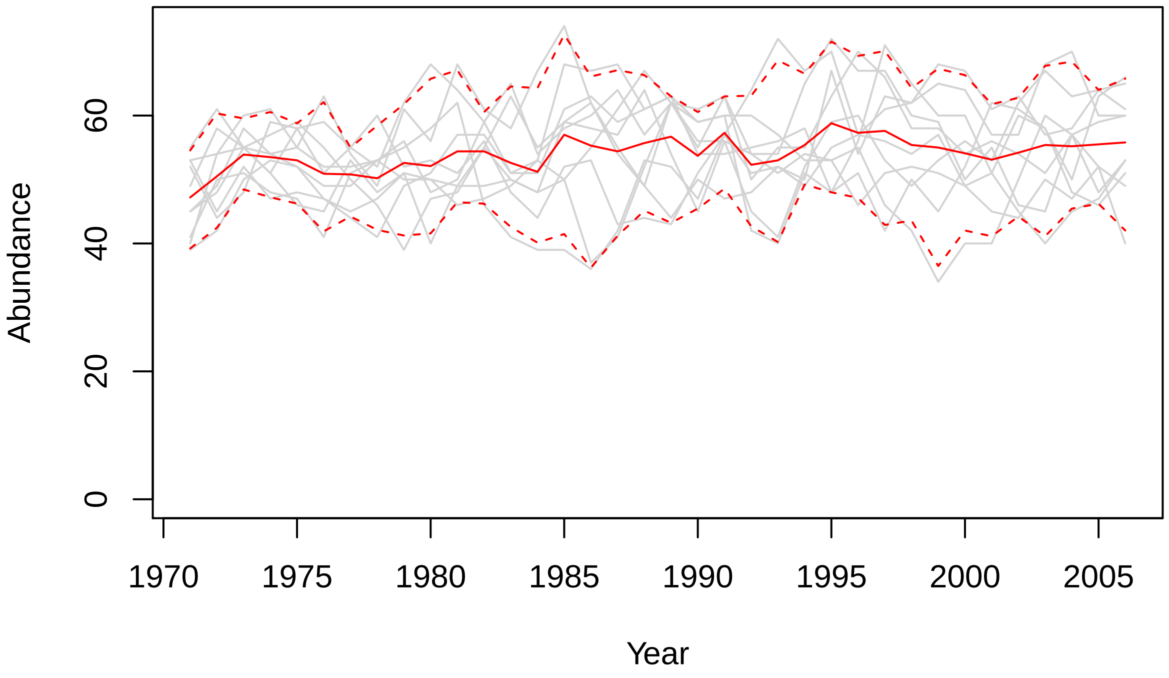
```
head(SongEvo1$all.inds, 5)
#>                    coordinates id age  trait        x1       y1
#> I1.T1.1 (-122.4818, 37.80545)  1   2 4004.8 -122.4818 37.80545
#> I1.T1.2 (-122.4598, 37.79643)  2   2 3765.0 -122.4598 37.79643
#> I1.T1.3 (-122.4773, 37.79265)  3   2 3237.4 -122.4773 37.79265
#> I1.T1.4  (-122.4489, 37.7979)  4   2 3621.1 -122.4489 37.79790
#> I1.T1.5 (-122.4628, 37.80409)  5   2 3285.4 -122.4628 37.80409
#>         male.fledglings territory father x0 y0 timestep iteration
#> I1.T1.1               1         1      0  0  0        1         1
#> I1.T1.2               1         1      0  0  0        1         1
#> I1.T1.3               2         1      0  0  0        1         1
#> I1.T1.4               1         1      0  0  0        1         1
#> I1.T1.5               0         1      0  0  0        1         1
```

Simulated population size

We see that the simulated population size remains relatively stable over the course of 36 years. This code uses the summary.results array.

```
plot(SongEvo1$summary.results[1, , "sample.n"], xlab="Year", ylab="Abundance", type="n",
    xaxt="n", ylim=c(0, max(SongEvo1$summary.results[, , "sample.n"], na.rm=TRUE)))
axis(side=1, at=seq(0, 40, by=5), labels=seq(1970, 2010, by=5))
```

```
    for(p in 1:iteration){
        lines(SongEvo1$summary.results[p, , "sample.n"], col="light gray")
        }
n.mean <- apply(SongEvo1$summary.results[, , "sample.n"], 2, mean, na.rm=TRUE)
lines(n.mean, col="red")

#Plot 95% quantiles
quant.means <- apply (SongEvo1$summary.results[, , "sample.n"], MARGIN=2, quantile,
    probs=c(0.975, 0.025), R=600, na.rm=TRUE)
lines(quant.means[1,], col="red", lty=2)
lines(quant.means[2,], col="red", lty=2)
```



Load Hmisc package for plotting functions.

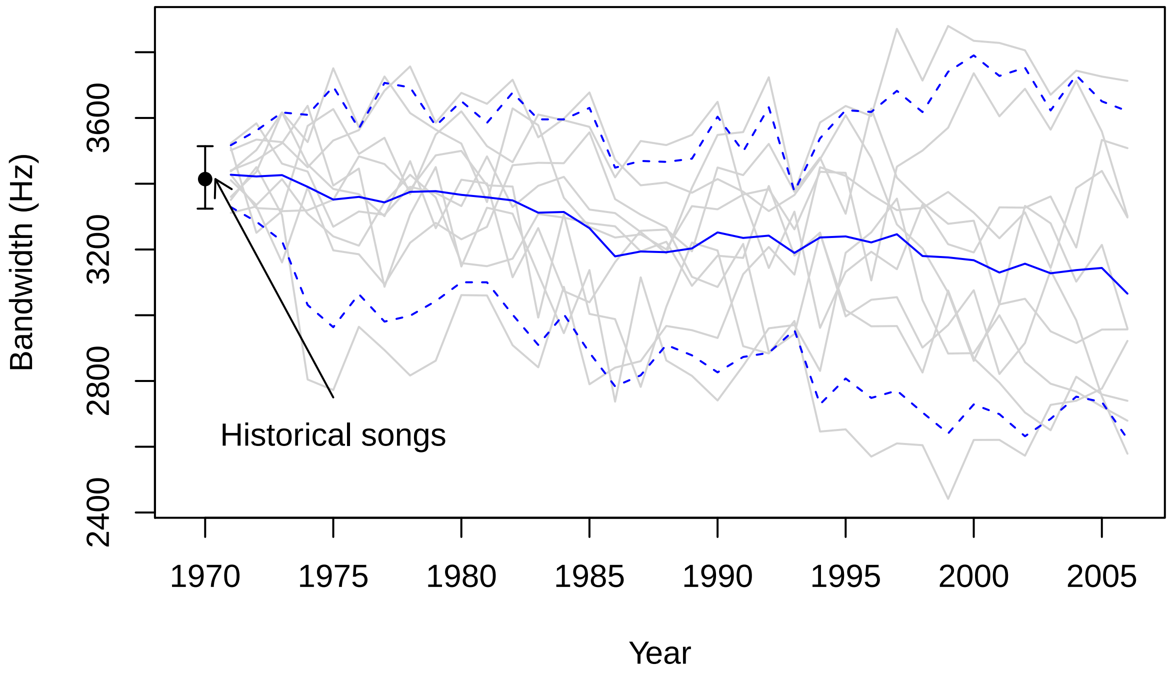
```
library("Hmisc")
```

Simulated trait values

We see that the mean trait values per iteration varied widely, though mean trait values over all iterations remained relatively stable. This code uses the summary.results array.

```
plot(SongEvo1$summary.results[1, , "trait.pop.mean"], xlab="Year", ylab="Bandwidth (Hz)",
    xaxt="n", type="n", xlim=c(-0.5, 36),
    ylim=c(min(SongEvo1$summary.results[, , "trait.pop.mean"], na.rm=TRUE),
    max(SongEvo1$summary.results[, , "trait.pop.mean"], na.rm=TRUE)))
    for(p in 1:iteration){
        lines(SongEvo1$summary.results[p, , "trait.pop.mean"], col="light gray")
        }
freq.mean <- apply(SongEvo1$summary.results[, , "trait.pop.mean"], 2, mean, na.rm=TRUE)
lines(freq.mean, col="blue")
axis(side=1, at=seq(0, 35, by=5), labels=seq(1970, 2005, by=5))#, tcl=-0.25, mgp=c(2,0.5,0))

#Plot 95% quantiles
```

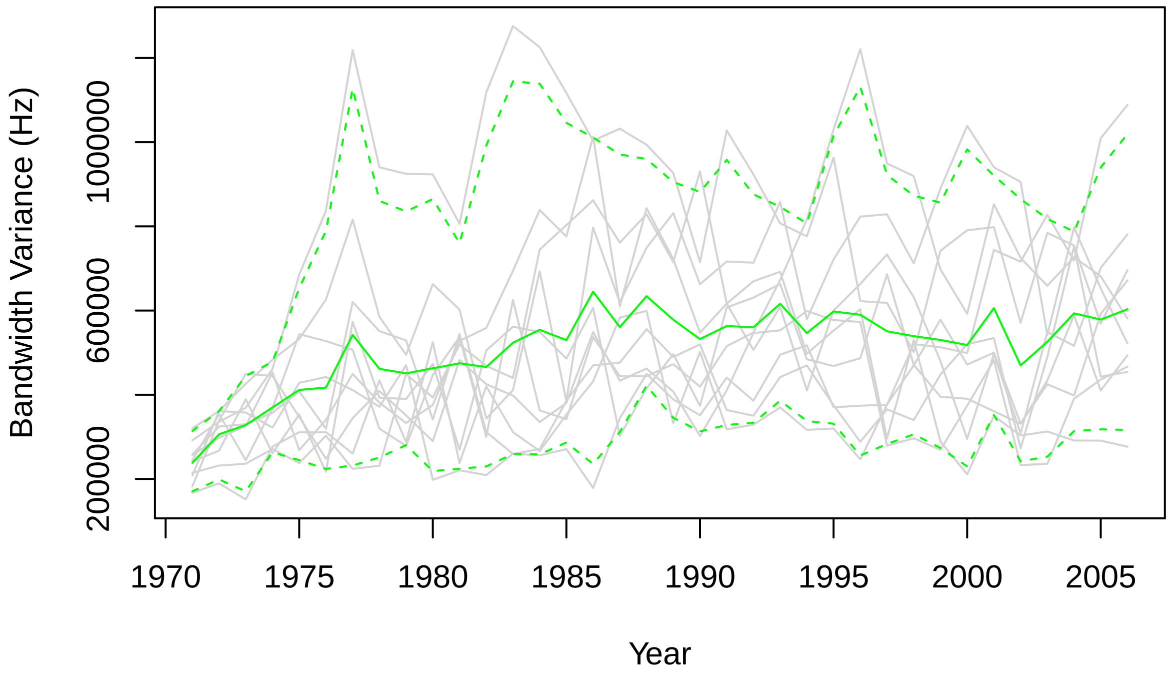
```r
quant.means <- apply (SongEvo1$summary.results[, , "trait.pop.mean"], MARGIN=2, quantile,
    probs=c(0.95, 0.05), R=600, na.rm=TRUE)
lines(quant.means[1,], col="blue", lty=2)
lines(quant.means[2,], col="blue", lty=2)

#plot mean and CI for historic songs.
 #plot original song values
library("boot")
#>
#> Attaching package: 'boot'
#> The following object is masked from 'package:survival':
#>
#>     aml
#> The following object is masked from 'package:lattice':
#>
#>     melanoma
sample.mean <- function(d, x) {
    mean(d[x])
}
boot_hist <- boot(starting.trait, statistic=sample.mean, R=100)#, strata=mn.res$iteration)
ci.hist <- boot.ci(boot_hist, conf=0.95, type="basic")
low <- ci.hist$basic[4]
high <- ci.hist$basic[5]
points(0, mean(starting.trait), pch=20, cex=0.6, col="black")
errbar(x=0, y=mean(starting.trait), high, low, add=TRUE)
 #text and arrows
text(x=5, y=2720, labels="Historical songs", pos=1)
arrows(x0=5, y0=2750, x1=0.4, y1=mean(starting.trait), length=0.1)
```



Trait variance

We see that variance for each iteration per year increased in the first few years and then stabilized. This code uses the summary.results array.

```
 #plot variance for each iteration per year
plot(SongEvo1$summary.results[1, , "trait.pop.variance"], xlab="Year",
    ylab="Bandwidth Variance (Hz)", type="n", xaxt="n",
    ylim=c(min(SongEvo1$summary.results[, , "trait.pop.variance"], na.rm=TRUE),
    max(SongEvo1$summary.results[, , "trait.pop.variance"], na.rm=TRUE)))
axis(side=1, at=seq(0, 40, by=5), labels=seq(1970, 2010, by=5))
    for(p in 1:iteration){
        lines(SongEvo1$summary.results[p, , "trait.pop.variance"], col="light gray")
        }
n.mean <- apply(SongEvo1$summary.results[, , "trait.pop.variance"], 2, mean, na.rm=TRUE)
lines(n.mean, col="green")

#Plot 95% quantiles
quant.means <- apply (SongEvo1$summary.results[, , "trait.pop.variance"], MARGIN=2, quantile,
    probs=c(0.975, 0.025), R=600, na.rm=TRUE)
lines(quant.means[1,], col="green", lty=2)
lines(quant.means[2,], col="green", lty=2)
```



Maps

The simulation results include geographical coordinates and are in a standard spatial data format, thus allowing calculation of a wide variety of spatial statistics.

Load packages for making maps.

```
library("sp")
library("reshape2")
library("lattice")
```

Convert data frame from long to wide format. This is necessary for making a multi-panel plot.

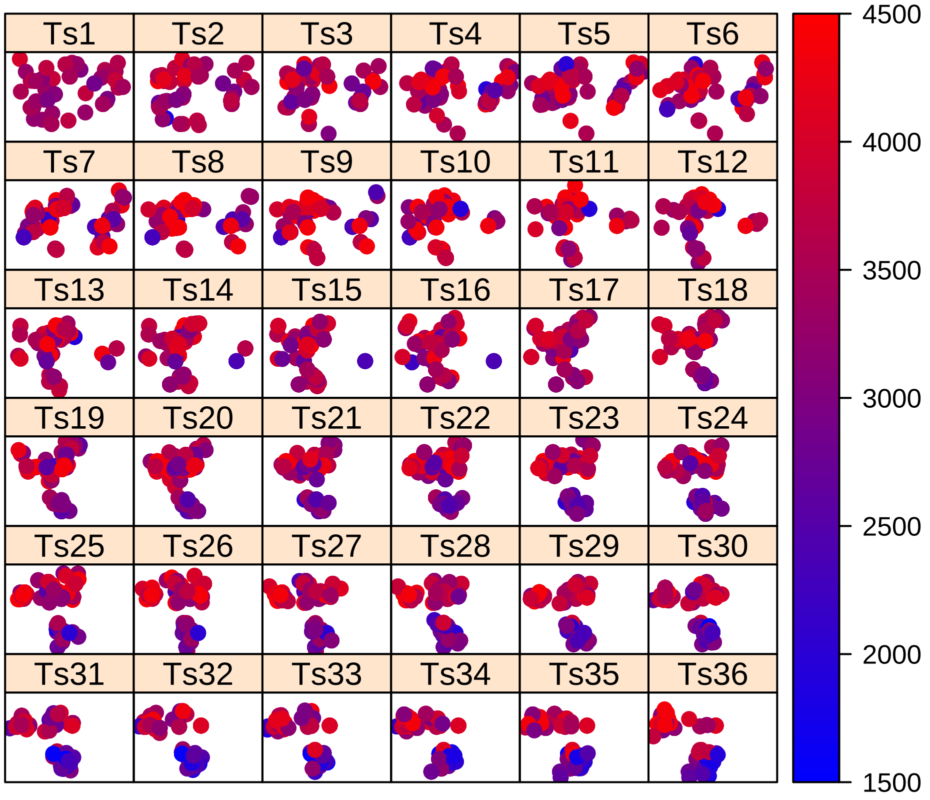
```r
all.inds1 <- subset(SongEvo1$all.inds, iteration==1)
w <- dcast(as.data.frame(all.inds1), id ~ timestep, value.var="trait", fill=0)
all.inds1w <- merge(all.inds1, w, by="id")
names(all.inds1w) <- c(names(all.inds1), paste("Ts", seq(1:years), sep=""))
```

Create a function to generate a continuous color palette–we will use the palette in the next call to make color ramp to represent the trait value.

```r
rbPal <- colorRampPalette(c('blue','red')) #Create a function to generate a continuous color palette
```

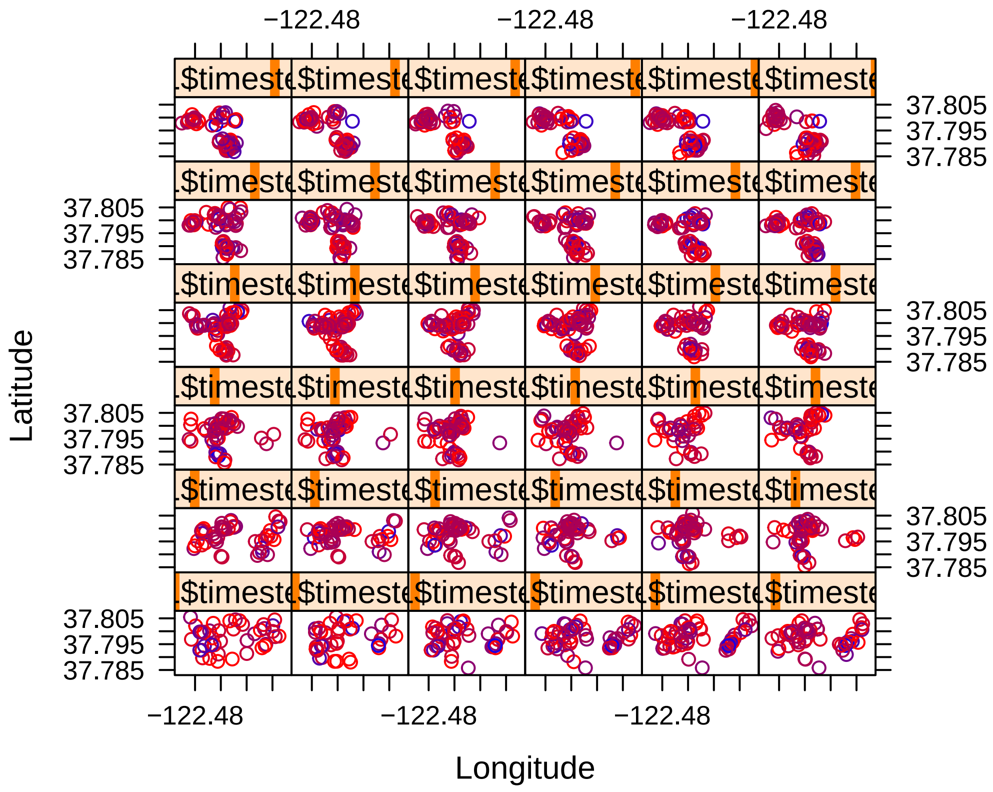
Plot maps, including a separate panel for each timestep (each of 36 years). Our example shows that individuals move across the landscape and that regional dialects evolve and move. The x-axis is longitude, the y-axis is latitude, and the color ramp indicates trill bandwidth in Hz.

```r
spplot(all.inds1w[,-c(1:ncol(all.inds1))], as.table=TRUE,
    cuts=c(0, seq(from=1500, to=4500, by=10)), ylab="",
    col.regions=c("transparent", rbPal(1000)),
    #cuts specifies that the first level (e.g. <1500) is transparent.
colorkey=list(
    right=list(
          fun=draw.colorkey,
          args=list(
                key=list(
                at=seq(1500, 4500, 10),
                col=rbPal(1000),
                labels=list(
                at=c(1500, 2000, 2500, 3000, 3500, 4000, 4500),
                labels=c("1500", "2000", "2500", "3000", "3500", "4000", "4500")
                )
                )
                )
            )
    )
)
```



In addition, you can plot simpler multi-panel maps that do not take advantage of the spatial data class.

```
 #Lattice plot (not as a spatial frame)
it1 <- subset(SongEvo1$all.inds, iteration==1)
rbPal <- colorRampPalette(c('blue','red')) #Create a function to generate a continuous color palette
it1$Col <- rbPal(10)[as.numeric(cut(it1$trait, breaks = 10))]
xyplot(it1$y1~it1$x1 | it1$timestep, groups=it1$trait, asp="iso", col=it1$Col,
    xlab="Longitude", ylab="Latitude")
```



Test model sensitivity with `par.sens()`

This function allows testing the sensitivity of SongEvo to different parameter values.

Specify and call `par.sens()`

Here we test the sensitivity of the Acquire a Territory submodel to variation in territory turnover rates, ranging from 0.8–1.2 times the published rate (40–60% of territories turned over). The call for the par.sens function has a format similar to SongEvo. The user specifies the parameter to test and the range of values for that parameter. The function currently allows examination of only one parameter at a time and requires at least two iterations.

```
parm <- "terr.turnover"
par.range = seq(from=0.4, to=0.6, by=0.05)
sens.results <- NULL
```

Now we call the par.sens function with our specifications.

```
extra_parms <- list(init.inds = init.inds,
                    timestep = 1,
                    n.territories = nrow(init.inds),
                    learning.method = "integrate",
                    integrate.dist = 0.1,
                    lifespan = NA,
                    terr.turnover = 0.5,
                    mate.comp = FALSE,
                    prin = FALSE,
                    all = TRUE)
global_parms_key <- which(!names(glo.parms) %in% names(extra_parms))
```

```
extra_parms[names(glo.parms[global_parms_key])]=glo.parms[global_parms_key]
par.sens1 <- par.sens(parm = parm, par.range = par.range,
                      iteration = iteration, steps = years, mate.comp = FALSE,
                      fixed_parms=extra_parms[names(extra_parms)!=parm], all = TRUE)
#> [1] "terr.turnover =  0.4"
#> [1] "terr.turnover =  0.45"
#> [1] "terr.turnover =  0.5"
#> [1] "terr.turnover =  0.55"
#> [1] "terr.turnover =  0.6"
```

Examine par.sens results

Examine results objects, which include two arrays:

The first array, `sens.results`, contains the SongEvo model results for each parameter. It has the following dimensions:

```
dimnames(par.sens1$sens.results)
#> [[1]]
#>  [1] "iteration 1"  "iteration 2"  "iteration 3"  "iteration 4"
#>  [5] "iteration 5"  "iteration 6"  "iteration 7"  "iteration 8"
#>  [9] "iteration 9"  "iteration 10"
#>
#> [[2]]
#>  [1] "1"  "2"  "3"  "4"  "5"  "6"  "7"  "8"  "9"  "10" "11" "12" "13" "14"
#> [15] "15" "16" "17" "18" "19" "20" "21" "22" "23" "24" "25" "26" "27" "28"
#> [29] "29" "30" "31" "32" "33" "34" "35" "36"
#>
#> [[3]]
#> [1] "sample.n"           "trait.pop.mean"     "trait.pop.variance"
#> [4] "lci"                "uci"
#>
#> [[4]]
#> [1] "par.val 0.4"  "par.val 0.45" "par.val 0.5"  "par.val 0.55"
#> [5] "par.val 0.6"
```

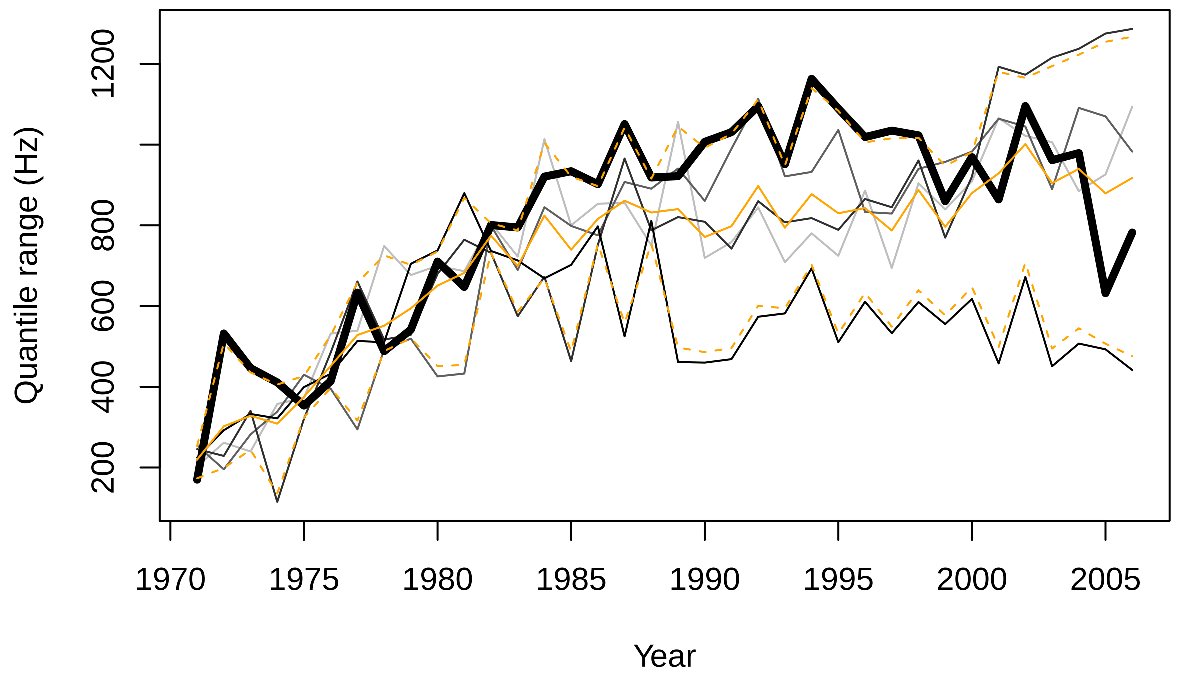
The second array, `sens.results.diff` contains the quantile range of trait values across iterations within a parameter value. It has the following dimensions:

```
dimnames(par.sens1$sens.results.diff)
#> [[1]]
#> [1] "par.val 0.4"  "par.val 0.45" "par.val 0.5"  "par.val 0.55"
#> [5] "par.val 0.6"
#>
#> [[2]]
#>  [1] "Quantile diff 1"  "Quantile diff 2"  "Quantile diff 3"
#>  [4] "Quantile diff 4"  "Quantile diff 5"  "Quantile diff 6"
#>  [7] "Quantile diff 7"  "Quantile diff 8"  "Quantile diff 9"
#> [10] "Quantile diff 10" "Quantile diff 11" "Quantile diff 12"
#> [13] "Quantile diff 13" "Quantile diff 14" "Quantile diff 15"
#> [16] "Quantile diff 16" "Quantile diff 17" "Quantile diff 18"
#> [19] "Quantile diff 19" "Quantile diff 20" "Quantile diff 21"
#> [22] "Quantile diff 22" "Quantile diff 23" "Quantile diff 24"
#> [25] "Quantile diff 25" "Quantile diff 26" "Quantile diff 27"
#> [28] "Quantile diff 28" "Quantile diff 29" "Quantile diff 30"
#> [31] "Quantile diff 31" "Quantile diff 32" "Quantile diff 33"
#> [34] "Quantile diff 34" "Quantile diff 35" "Quantile diff 36"
```

To assess sensitivity of SongEvo to a range of parameter values, plot the range in trait quantiles per year by the parameter value. We see that territory turnover values of 0.4–0.6 provided means and quantile ranges of trill bandwidths that are similar to those obtained with the published estimate of 0.5, indicating that the Acquire a Territory submodel is robust to realistic variation in those parameter values.

In the figure, solid gray and black lines show the quantile range of song frequency per year over all iterations as parameterized with the published territory turnover rate (0.5; thick black line) and a range of values from 0.4 to 0.6 (in steps of 0.05, light to dark gray). Orange lines show the mean and 2.5th and 97.5th quantiles of all quantile ranges.

```
 #plot of range in trait quantiles by year by parameter value
plot(1:years, par.sens1$sens.results.diff[1,], ylim=c(min(par.sens1$sens.results.diff,
    na.rm=TRUE), max(par.sens1$sens.results.diff, na.rm=TRUE)), type="l",
    ylab="Quantile range (Hz)", xlab="Year", col="transparent", xaxt="n")
axis(side=1, at=seq(0, 35, by=5), labels=seq(1970, 2005, by=5))

  #Make a continuous color ramp from gray to black
grbkPal <- colorRampPalette(c('gray','black'))

  #Plot a line for each parameter value
for(i in 1:length(par.range)){
lines(1:years, par.sens1$sens.results.diff[i,], type="l",
    col=grbkPal(length(par.range))[i])
}

  #Plot values from published parameter values
lines(1:years, par.sens1$sens.results.diff[2,], type="l", col="black", lwd=4)

  #Calculate and plot mean and quantiles
quant.mean <- apply(par.sens1$sens.results.diff, 2, mean, na.rm=TRUE)
lines(quant.mean, col="orange")

#Plot 95% quantiles (which are similar to credible intervals)
  #95% quantiles of population means (narrower)
quant.means <- apply (par.sens1$sens.results.diff, MARGIN=2, quantile,
    probs=c(0.975, 0.025), R=600, na.rm=TRUE)
lines(quant.means[1,], col="orange", lty=2)
lines(quant.means[2,], col="orange", lty=2)
```



Optimize parameter values with `par.opt()`

This function follows par.sens to help users optimize values for imperfectly known parameters for SongEvo. The goals are to maximize accuracy and precision of model prediction. Accuracy is quantified by three different approaches: i) the mean of absolute residuals of the predicted population mean values in relation to target data (e.g. observed or hypothetical values (smaller absolute residuals indicate a more accurate model)), ii) the difference between the bootstrapped mean of predicted population means and the mean of the target data, and iii) the proportion of simulated population trait means that fall within (i.e. are "contained by") the confidence intervals of the target data (a higher proportion indicates greater accuracy). Precision is measured with the residuals of the predicted population variance to the variance of target data (smaller residuals indicate a more precise model).

Prepare current song values

```
target.data <- subset(song.data, Population=="PRBO" & Year==2005)$Trill.FBW
```

Specify and call `par.opt()`

Users specify the timestep ("ts") at which to compare simulated trait values to target trait data ("target.data") and save the results in an object (called `par.opt1` here).

```
ts <- years
par.opt1 <- par.opt(sens.results=par.sens1$sens.results, ts=ts,
    target.data=target.data, par.range=par.range)
```

Examine results objects (residuals and target match).

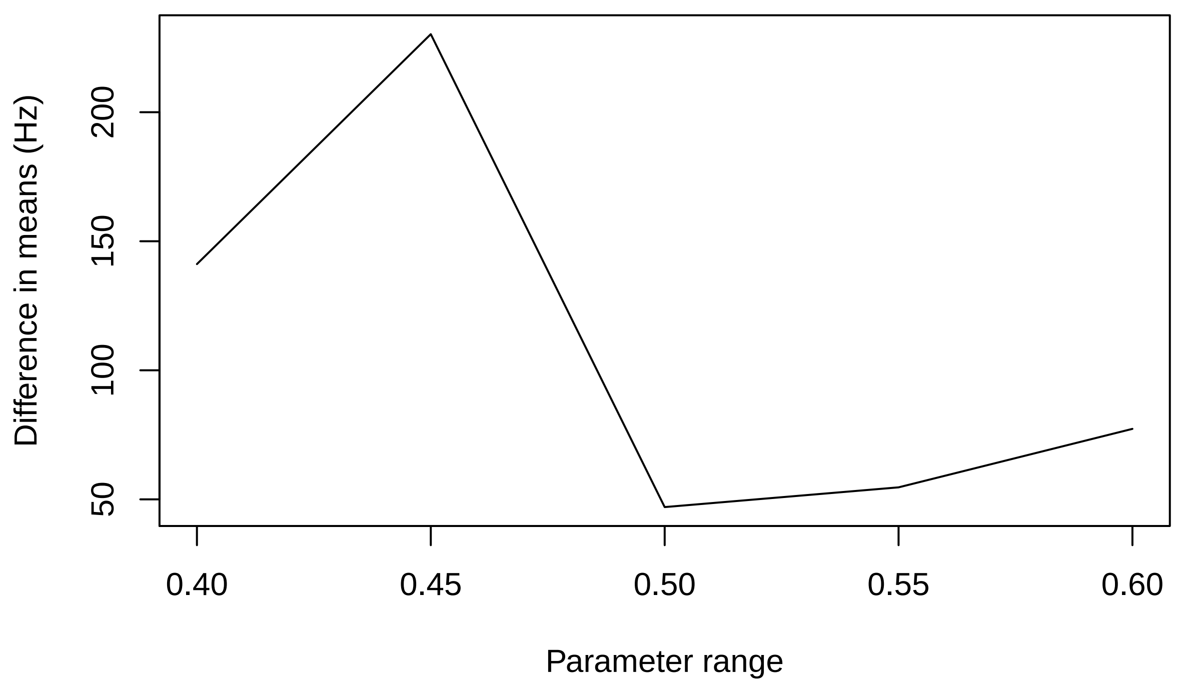
```
par.opt1$Residuals
#> , , Residuals of mean
#>
#>               Iteration 1 Iteration 2 Iteration 3 Iteration 4 Iteration 5
#> par.val 0.4     282.22070    58.66497    359.3872   108.27770   290.09231
#> par.val 0.45   251.40714   400.22939    654.5811   342.05936   653.81619
#> par.val 0.5    664.44194   326.75904    293.8925   614.36130    60.68993
#> par.val 0.55   264.39744   221.78145    590.5065   302.69986   871.66153
#> par.val 0.6     30.01236    62.12094    212.9996    33.40431   117.56523
#>               Iteration 6 Iteration 7 Iteration 8 Iteration 9 Iteration 10
#> par.val 0.4    933.24316   143.20897   336.68528   569.38379    269.13579
#> par.val 0.45    69.41577   331.73598    31.60272   175.96474     54.60890
#> par.val 0.5     24.42922   100.16414   310.42100    89.73264     18.88416
#> par.val 0.55   636.39207   425.48523   107.47236   226.64881    161.94380
#> par.val 0.6    389.80569    85.44882    13.22906   102.16536    258.96535
#>
#> , , Residuals of variance
#>
#>               Iteration 1 Iteration 2 Iteration 3 Iteration 4 Iteration 5
#> par.val 0.4      499709.1    339545.8    403112.0    499604.7    587900.4
#> par.val 0.45     477585.6    579600.2    403598.9    360111.2    771465.5
#> par.val 0.5      273831.1    400330.2    357432.0    224393.5    266520.3
#> par.val 0.55     488033.6    287856.5    273198.7    371437.3    371773.0
#> par.val 0.6      659242.8    379145.9    412487.0    303742.7    789671.2
#>               Iteration 6 Iteration 7 Iteration 8 Iteration 9 Iteration 10
#> par.val 0.4      389806.6    674064.7    460203.4    431266.6     460082.9
#> par.val 0.45     273138.4    444957.3   1062435.7    417110.1     688118.4
#> par.val 0.5      455068.2    303186.7    840573.8    337377.1     277133.2
#> par.val 0.55     183305.9    512225.1    903324.2   1014289.8     422009.9
#> par.val 0.6      276834.2    921140.0    560038.9    871313.1     858341.2
par.opt1$Target.match
#>               Difference in means Proportion contained
#> par.val 0.4             141.14826                  0.1
#> par.val 0.45            230.22370                  0.3
#> par.val 0.5              47.00347                  0.3
#> par.val 0.55             54.64532                  0.0
#> par.val 0.6              77.29888                  0.4
```

Plot results of `par.opt()`

Accuracy

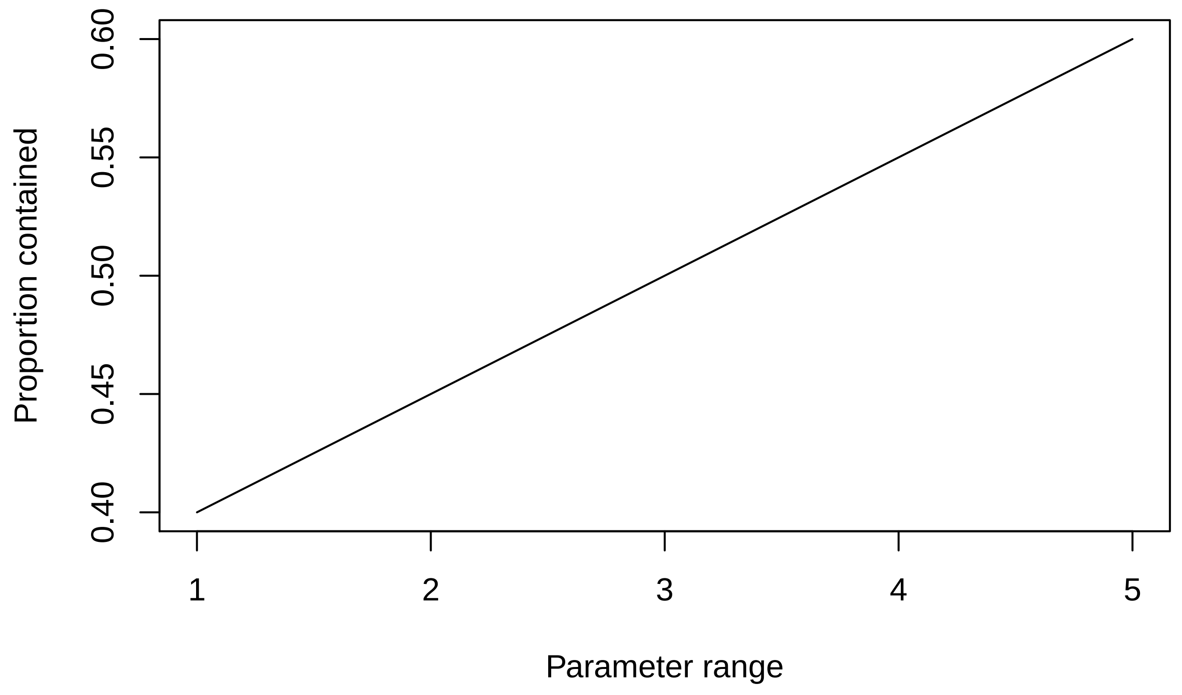
1. Difference in means.

```
plot(par.range, par.opt1$Target.match[,1], type="l", xlab="Parameter range",
    ylab="Difference in means (Hz)")
```



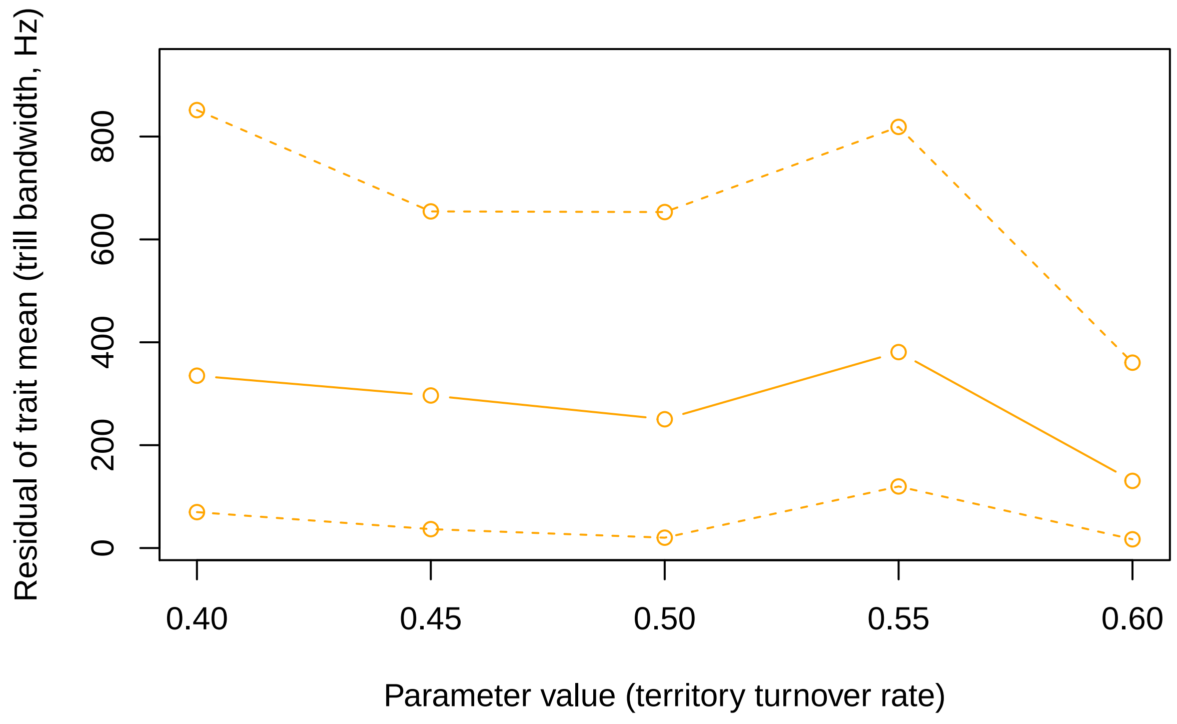
2. Plot proportion contained.

```
plot(par.range, par.opt1$Prop.contained, type="l", xlab="Parameter range",
    ylab="Proportion contained")
```



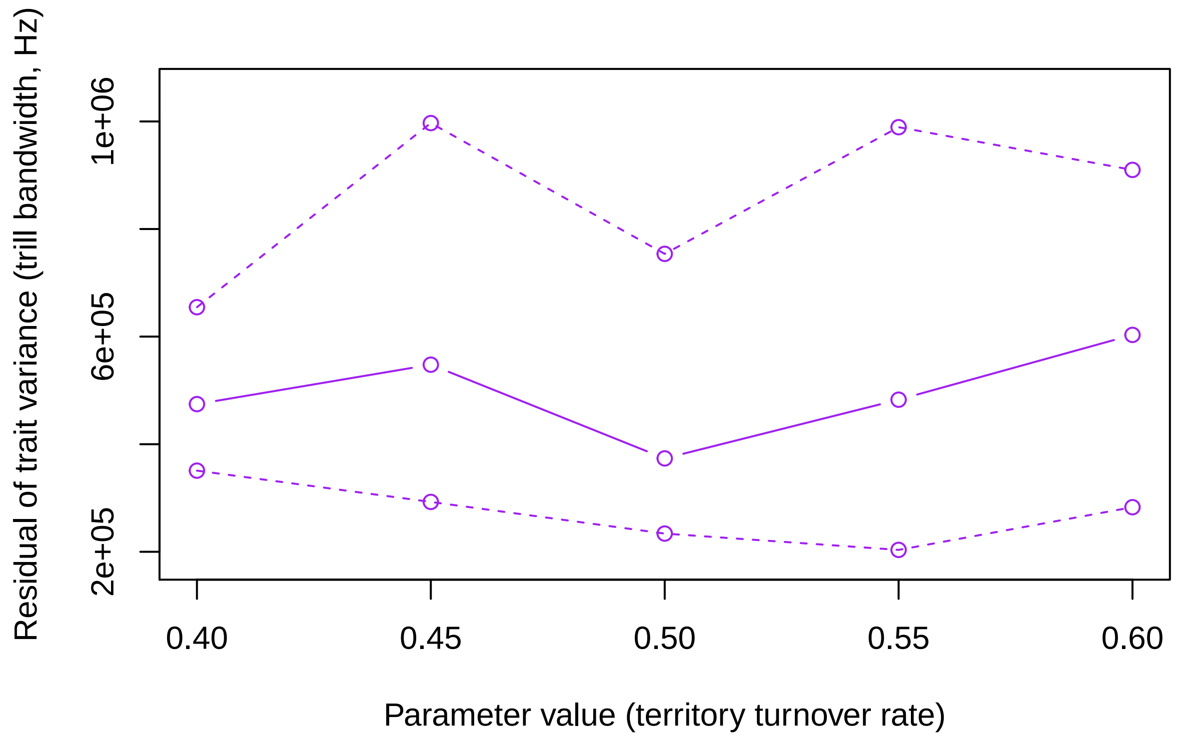
3. Calculate and plot mean and quantiles of residuals of mean trait values.

```
res.mean.means <- apply(par.opt1$Residuals[, , 1], MARGIN=1, mean, na.rm=TRUE)
res.mean.quants <- apply (par.opt1$Residuals[, , 1], MARGIN=1, quantile,
    probs=c(0.975, 0.025), R=600, na.rm=TRUE)
plot(par.range, res.mean.means, col="orange", ylim=c(min(par.opt1$Residuals[,,1],
    na.rm=TRUE), max(par.opt1$Residuals[,,1], na.rm=TRUE)), type="b",
    xlab="Parameter value (territory turnover rate)",
    ylab="Residual of trait mean (trill bandwidth, Hz)")
points(par.range, res.mean.quants[1,], col="orange")
points(par.range, res.mean.quants[2,], col="orange")
lines(par.range, res.mean.quants[1,], col="orange", lty=2)
lines(par.range, res.mean.quants[2,], col="orange", lty=2)
```



Precision

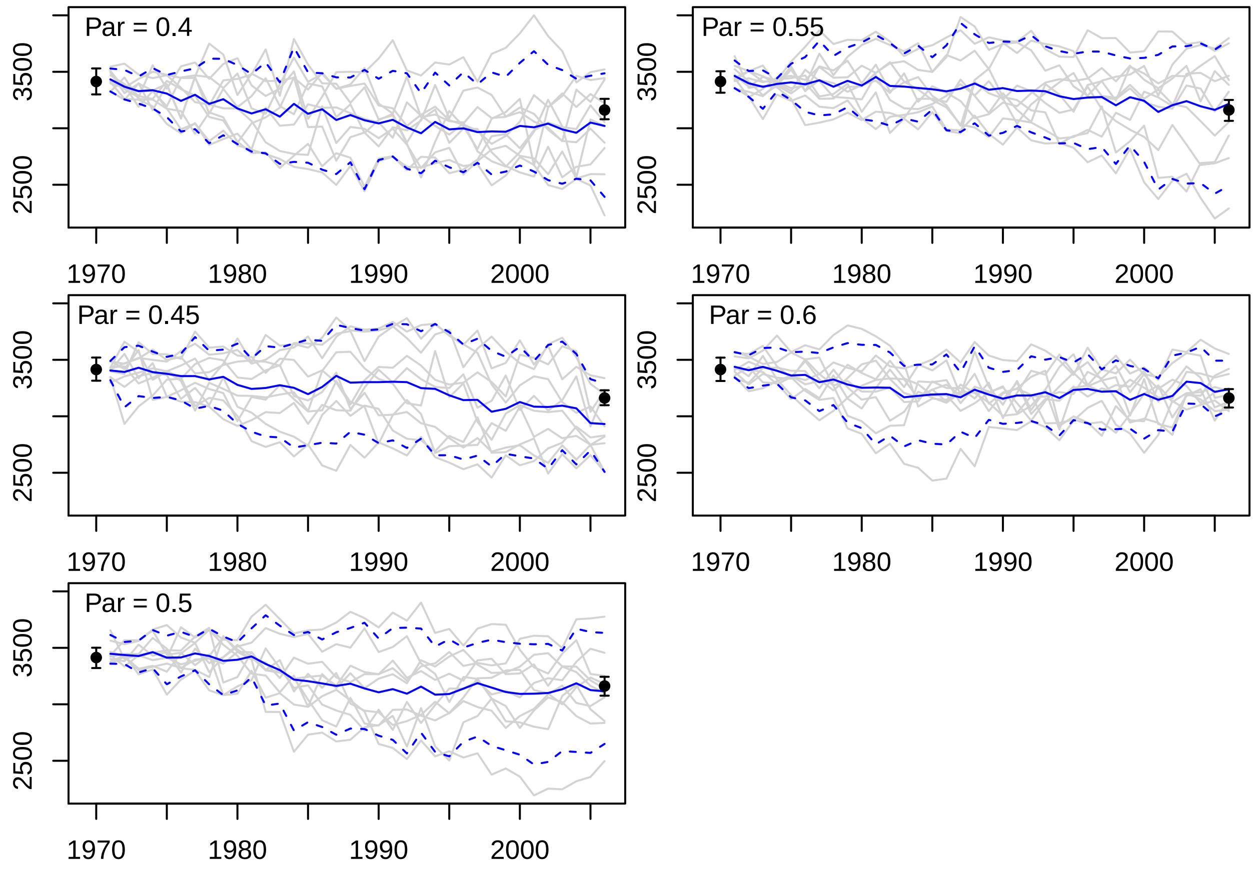
```
#Calculate and plot mean and quantiles of residuals of variance of trait values
res.var.mean <- apply(par.opt1$Residuals[, , 2], MARGIN=1, mean, na.rm=TRUE)
res.var.quants <- apply (par.opt1$Residuals[, , 2], MARGIN=1, quantile,
    probs=c(0.975, 0.025), R=600, na.rm=TRUE)
plot(par.range, res.var.mean, col="purple",
    ylim=c(min(par.opt1$Residuals[,,2], na.rm=TRUE),
    max(par.opt1$Residuals[,,2], na.rm=TRUE)), type="b",
    xlab="Parameter value (territory turnover rate)",
    ylab="Residual of trait variance (trill bandwidth, Hz)")
points(par.range, res.var.quants[1,], col="purple")
points(par.range, res.var.quants[2,], col="purple")
lines(par.range, res.var.quants[1,], col="purple", lty=2)
lines(par.range, res.var.quants[2,], col="purple", lty=2)
```



Visual inspection of accuracy and precision: plot trait values for range of parameters

```
par(mfcol=c(3,2),
    mar=c(2.1, 2.1, 0.1, 0.1),
    cex=0.8)
for(i in 1:length(par.range)){
plot(par.sens1$sens.results[ , , "trait.pop.mean", ], xlab="Year", ylab="Bandwidth (Hz)",
    xaxt="n", type="n", xlim=c(-0.5, years),
    ylim=c(min(par.sens1$sens.results[ , , "trait.pop.mean", ], na.rm=TRUE),
    max(par.sens1$sens.results[ , , "trait.pop.mean", ], na.rm=TRUE)))
    for(p in 1:iteration){
        lines(par.sens1$sens.results[p, , "trait.pop.mean", i], col="light gray")
        }
freq.mean <- apply(par.sens1$sens.results[, , "trait.pop.mean", i], 2, mean, na.rm=TRUE)
lines(freq.mean, col="blue")
axis(side=1, at=seq(0, 35, by=5), labels=seq(1970, 2005, by=5))

#Plot 95% quantiles
quant.means <- apply (par.sens1$sens.results[, , "trait.pop.mean", i], MARGIN=2, quantile,
    probs=c(0.95, 0.05), R=600, na.rm=TRUE)
lines(quant.means[1,], col="blue", lty=2)
lines(quant.means[2,], col="blue", lty=2)

#plot mean and CI for historic songs.
 #plot original song values
library("boot")
sample.mean <- function(d, x) {
    mean(d[x])
}
boot_hist <- boot(starting.trait, statistic=sample.mean, R=100)#, strata=mm.res$iteration)
```

```
ci.hist <- boot.ci(boot_hist, conf=0.95, type="basic")
low <- ci.hist$basic[4]
high <- ci.hist$basic[5]
points(0, mean(starting.trait), pch=20, cex=0.6, col="black")
library("Hmisc")
errbar(x=0, y=mean(starting.trait), high, low, add=TRUE)

 #plot current song values
library("boot")
sample.mean <- function(d, x) {
    mean(d[x])
}
boot_curr <- boot(target.data, statistic=sample.mean, R=100)#, strata=mn.res$iteration)
ci.curr <- boot.ci(boot_curr, conf=0.95, type="basic")
low <- ci.curr$basic[4]
high <- ci.curr$basic[5]
points(years, mean(target.data), pch=20, cex=0.6, col="black")
library("Hmisc")
errbar(x=years, y=mean(target.data), high, low, add=TRUE)

  #plot panel title
text(x=3, y=max(par.sens1$sens.results[ , , "trait.pop.mean", ], na.rm=TRUE)-100,
    labels=paste("Par = ", par.range[i], sep=""))
}
```



Model validation with `mod.val()`

This function allows users to assess the validity of the specified model by testing model performance with a population different from the population used to build the model. The user first runs SongEvo with initial trait values from the validation population. `mod.val()` uses the summary.results array from SongEvo, along with target values from a specified timestep, to calculate the same three measures of accuracy and one measure of precision that are calculated in par.opt.

We parameterized SongEvo with initial song data from Schooner Bay, CA in 1969, and then compared simulated data to target (i.e. observed) data in 2005.

Prepare initial song data for Schooner Bay.

```
starting.trait <- subset(song.data, Population=="Schooner" & Year==1969)$Trill.FBW
starting.trait2 <- c(starting.trait, rnorm(n.territories-length(starting.trait),
    mean=mean(starting.trait), sd=sd(starting.trait)))

init.inds <- data.frame(id = seq(1:n.territories), age = 2, trait = starting.trait2)
init.inds$x1 <-  round(runif(n.territories, min=-122.481858, max=-122.447270), digits=8)
init.inds$y1 <-  round(runif(n.territories, min=37.787768, max=37.805645), digits=8)
```

Specify and call SongEvo() with validation data

```
iteration <- 10
years <- 36
timestep <- 1
terr.turnover <- 0.5

SongEvo2 <- SongEvo(init.inds = init.inds, iteration = iteration, steps = years,
    timestep = timestep, n.territories = n.territories, terr.turnover = terr.turnover,
    learning.method = learning.method, integrate.dist = integrate.dist,
    learning.error.d = learning.error.d, learning.error.sd = learning.error.sd,
    mortality.a = mortality.a, mortality.j = mortality.j, lifespan = lifespan,
    phys.lim.min = phys.lim.min, phys.lim.max = phys.lim.max,
    male.fledge.n.mean = male.fledge.n.mean, male.fledge.n.sd = male.fledge.n.sd,
    male.fledge.n = male.fledge.n, disp.age = disp.age,
    disp.distance.mean = disp.distance.mean, disp.distance.sd = disp.distance.sd,
    mate.comp = mate.comp, prin = prin, all)
```

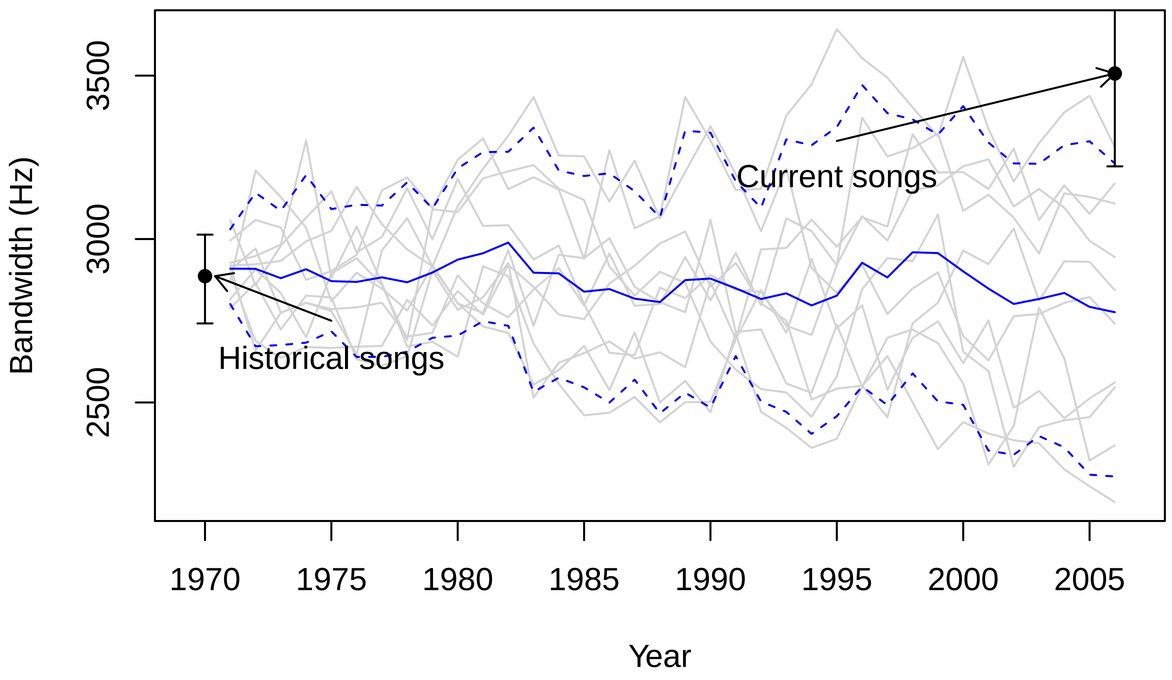
Specify and call mod.val

```
ts <- 36
target.data <- subset(song.data, Population=="Schooner" & Year==2005)$Trill.FBW
mod.val1 <- mod.val(summary.results=SongEvo2$summary.results, ts=ts,
    target.data=target.data)
```

Plot results from `mod.val()`

```
plot(SongEvo2$summary.results[1, , "trait.pop.mean"], xlab="Year", ylab="Bandwidth (Hz)",
    xaxt="n", type="n", xlim=c(-0.5, 36.5),
    ylim=c(min(SongEvo2$summary.results[, , "trait.pop.mean"], na.rm=TRUE),
    max(SongEvo2$summary.results[, , "trait.pop.mean"], na.rm=TRUE)))
    for(p in 1:iteration){
        lines(SongEvo2$summary.results[p, , "trait.pop.mean"], col="light gray")
        }
freq.mean <- apply(SongEvo2$summary.results[, , "trait.pop.mean"], 2, mean, na.rm=TRUE)
lines(freq.mean, col="blue")
axis(side=1, at=seq(0, 35, by=5), labels=seq(1970, 2005, by=5))
```

```r
#Plot 95% quantiles
quant.means <- apply (SongEvo2$summary.results[, , "trait.pop.mean"], MARGIN=2, quantile,
    probs=c(0.95, 0.05), R=600, na.rm=TRUE)
lines(quant.means[1,], col="blue", lty=2)
lines(quant.means[2,], col="blue", lty=2)

#plot mean and CI for historic songs.
 #plot original song values
library("boot")
sample.mean <- function(d, x) {
    mean(d[x])
}
boot_hist <- boot(starting.trait, statistic=sample.mean, R=100)
ci.hist <- boot.ci(boot_hist, conf=0.95, type="basic")
low <- ci.hist$basic[4]
high <- ci.hist$basic[5]
points(0, mean(starting.trait), pch=20, cex=0.6, col="black")
library("Hmisc")
errbar(x=0, y=mean(starting.trait), high, low, add=TRUE)

 #text and arrows
text(x=5, y=2720, labels="Historical songs", pos=1)
arrows(x0=5, y0=2750, x1=0.4, y1=mean(starting.trait), length=0.1)

 #plot current song values
library("boot")
sample.mean <- function(d, x) {
    mean(d[x])
}
boot_curr <- boot(target.data, statistic=sample.mean, R=100)
ci.curr <- boot.ci(boot_curr, conf=0.95, type="basic")
low <- ci.curr$basic[4]
high <- ci.curr$basic[5]
points(years, mean(target.data), pch=20, cex=0.6, col="black")
library("Hmisc")
errbar(x=years, y=mean(target.data), high, low, add=TRUE)

 #text and arrows
text(x=25, y=3100, labels="Current songs", pos=3)
arrows(x0=25, y0=3300, x1=36, y1=mean(target.data), length=0.1)
```



The model did reasonably well predicting trait evolution in the validation population, suggesting that it is valid for our purposes: the mean bandwidth was `abs(mean(target.data)-freq.mean)`Hz from the observed values, ~21% of predicted population means fell within the 95% confidence intervals of the observed data, and residuals of means (~545 Hz) and variances (~415181 Hz) were similar to those produced by the training data set.

Hypothesis testing with `h.test()`

This function allows hypothesis testing with SongEvo. To test if measured songs from two time points evolved through mechanisms described in the model (e.g. drift or selection), users initialize the model with historical data, parameterize the model based on their understanding of the mechanisms, and test if subsequently observed or predicted data match the simulated data. The output data list includes two measures of accuracy: the proportion of observed points that fall within the confidence intervals of the simulated data and the residuals between simulated and observed population trait means. Precision is measured as the residuals between simulated and observed population trait variances. We tested the hypothesis that songs of *Z. l. nuttalli* in Bear Valley, CA evolved through cultural drift from 1969 to 2005.

Prepare initial song data for Bear Valley.

```
starting.trait <- subset(song.data, Population=="Bear Valley" & Year==1969)$Trill.FBW
starting.trait2 <- c(starting.trait, rnorm(n.territories-length(starting.trait),
    mean=mean(starting.trait), sd=sd(starting.trait)))

init.inds <- data.frame(id = seq(1:n.territories), age = 2, trait = starting.trait2)
init.inds$x1 <-  round(runif(n.territories, min=-122.481858, max=-122.447270), digits=8)
init.inds$y1 <-  round(runif(n.territories, min=37.787768, max=37.805645), digits=8)
```

Specify and call SongEvo() with test data

```
SongEvo3 <- SongEvo(init.inds = init.inds, iteration = iteration, steps = years,
    timestep = timestep, n.territories = n.territories, terr.turnover = terr.turnover,
    learning.method = learning.method, integrate.dist = integrate.dist,
    learning.error.d = learning.error.d, learning.error.sd = learning.error.sd,
    mortality.a = mortality.a, mortality.j = mortality.j, lifespan = lifespan,
    phys.lim.min = phys.lim.min, phys.lim.max = phys.lim.max,
    male.fledge.n.mean = male.fledge.n.mean, male.fledge.n.sd = male.fledge.n.sd,
    male.fledge.n = male.fledge.n, disp.age = disp.age,
    disp.distance.mean = disp.distance.mean, disp.distance.sd = disp.distance.sd,
    mate.comp = mate.comp, prin = prin, all)
```

Specify and call `h.test()`

```
target.data <- subset(song.data, Population=="Bear Valley" & Year==2005)$Trill.FBW
h.test1 <- h.test(summary.results=SongEvo3$summary.results, ts=ts,
    target.data=target.data)
```

The output data list includes two measures of accuracy: the proportion of observed points that fall within the confidence intervals of the simulated data and the residuals between simulated and observed population trait means. Precision is measured as the residuals between simulated and observed population trait variances.

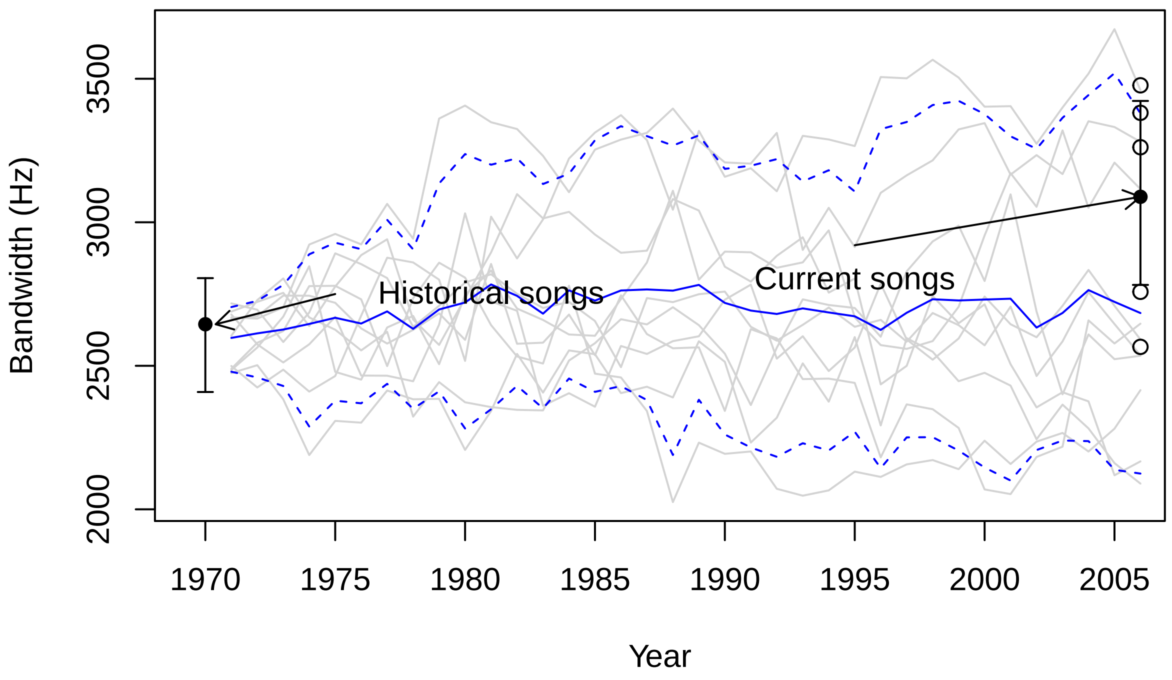
Eighty percent of the observed data fell within the central 95% of the simulated values, providing support for the hypothesis that cultural drift as described in this model is sufficient to describe the evolution of trill frequency bandwidth in this population.

```
h.test1
#> $Residuals
#>              Residuals of mean Residuals of variance
#> Iteration 1            26.8820              583502.6
#> Iteration 2           191.5151              281175.9
#> Iteration 3           371.4263              240718.7
#> Iteration 4           441.9115              662838.9
#> Iteration 5           673.6673              266263.3
#> Iteration 6           553.7866              755111.3
#> Iteration 7           999.1338              298078.0
#> Iteration 8           921.6738              343787.6
#> Iteration 9           496.9784              585446.2
#> Iteration 10          552.2382              547696.0
#>
#> $Prop.contained
#> [1] 0.6
```

We can plot simulated data in relation to measured data.

```
#Plot
plot(SongEvo3$summary.results[1, , "trait.pop.mean"], xlab="Year", ylab="Bandwidth (Hz)",
    xaxt="n", type="n", xlim=c(-0.5, 35.5),
    ylim=c(min(SongEvo3$summary.results[, , "trait.pop.mean"], na.rm=TRUE),
    max(SongEvo3$summary.results[, , "trait.pop.mean"], na.rm=TRUE)))
    for(p in 1:iteration){
        lines(SongEvo3$summary.results[p, , "trait.pop.mean"], col="light gray")
        }
freq.mean <- apply(SongEvo3$summary.results[, , "trait.pop.mean"], 2, mean, na.rm=TRUE)
lines(freq.mean, col="blue")
axis(side=1, at=seq(0, 35, by=5), labels=seq(1970, 2005, by=5))#, tcl=-0.25, mgp=c(2,0.5,0))

#Plot 95% quantiles (which are similar to credible intervals)
quant.means <- apply (SongEvo3$summary.results[, , "trait.pop.mean"], MARGIN=2, quantile,
    probs=c(0.95, 0.05), R=600, na.rm=TRUE)
lines(quant.means[1,], col="blue", lty=2)
```

```r
lines(quant.means[2,], col="blue", lty=2)

 #plot original song values
library("boot")
sample.mean <- function(d, x) {
    mean(d[x])
}
boot_hist <- boot(starting.trait, statistic=sample.mean, R=100)#, strata=mn.res$iteration)
ci.hist <- boot.ci(boot_hist, conf=0.95, type="basic")
low <- ci.hist$basic[4]
high <- ci.hist$basic[5]
points(0, mean(starting.trait), pch=20, cex=0.6, col="black")
library("Hmisc")
errbar(x=0, y=mean(starting.trait), high, low, add=TRUE)

 #plot current song values
points(rep(ts, length(target.data)), target.data)

library("boot")
sample.mean <- function(d, x) {
    mean(d[x])
}
boot_curr <- boot(target.data, statistic=sample.mean, R=100)#, strata=mn.res$iteration)
ci.curr <- boot.ci(boot_curr, conf=0.95, type="basic")
low <- ci.curr$basic[4]
high <- ci.curr$basic[5]
points(years, mean(target.data), pch=20, cex=0.6, col="black")
library("Hmisc")
errbar(x=years, y=mean(target.data), high, low, add=TRUE)

 #text and arrows
text(x=11, y=2850, labels="Historical songs", pos=1)
arrows(x0=5, y0=2750, x1=0.4, y1=mean(starting.trait), length=0.1)
text(x=25, y=2900, labels="Current songs", pos=1)
arrows(x0=25, y0=2920, x1=years, y1=mean(target.data), length=0.1)
```


Historical songs
Current songs
Bandwidth (Hz)
3500
3000
2500
2000
1970
1975
1980
1985
1990
1995
2000
2005
Year