

Phylogenetic comparative methods in fisheries science

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Phylogenetic comparative methods (PCM) are rarely in fisheries science, perhaps due to a lack of familiarity with methods and software among fisheries scientists. This underuse is surprising, given that fisheries science and management strongly depends on foundational results from comparative methods regarding fish productivity and life-history parameters, e.g., for defining proxies for biological reference points and informing hard-to-estimate demographic rates such as stock-recruit and natural mortality parameters.

Preparing the Then et al. mortality database

To demonstrate the potential role for PCM in fisheries science, we re-analyze a foundational dataset compiled by Then et al.. We specifically download the file “Mlifehist_ver1.0.csv” and then include a copy as a data object in package *phylosem* to simplify the following demonstration. This demonstration then provides basic syntax and output from PCM, showing the relationship between natural mortality rate, longevity, and growth parameters.

To do so, we first load a phylogeny for fishes using package *fishtree*, which includes several versions of a phylogeny for fishes developed by Rabosky et al.. We then associate all trait data with a tip label from that phylogeny, and provide convenient names for the modeled variables.

```
# Load packages
library(phylosem)
library(fishtree)

# Download tree
out = fishtree_complete_phylogeny()
tree = out[[1]]

# Load data object
data( Mlifehist_ver1_0 )
Data = Mlifehist_ver1_0

# Reformat to match tree$tip.label
Data$Genus_species = factor( paste0(Data$Genus, "_", Data$Species) )

# Drop duplicates ... not dealing with variation among stocks within species
Data = Data[match(unique(Data$Genus_species),Data$Genus_species), ]

# log-transform to simplify later syntax
Data = cbind( Data, "logM" = log(Data[, 'M']),
              "logK" = log(Data[, 'K']),
              "logtmax" = log(Data[, 'tmax']),
              "logLinf" = log(Data[, 'Linf']) )

# Identify species in both datasets
species_to_use = intersect( tree$tip.label, Data$Genus_species )
```

```

species_to_drop = setdiff( Data$Genus_species, tree$tip.label )

# Drop tips not present in trait-data
# Not strictly necessary, but helpful to simplify later plots
tree = ape::keep.tip( tree, tip=species_to_use )

# Drop trait-data not in phylogeny
# Necessary to define correlation among data
rows_to_use = which( Data$Genus_species %in% species_to_use )
Data = Data[rows_to_use,]

# Only include modeled variables in trait-data passed to phylosem
rownames(Data) = Data$Genus_species
Data = Data[,c('logM', 'logK', 'logtmax', 'logLinf')]

```

Fitting and selecting among phylogenetic structural equation models

We then define a path diagram specifying a set of linkages among variables. In the following, we use a path diagram that ensures that mortality rate is statistically independent of growth, conditional upon a measurement for longevity. This specification ensures that, if longevity is available, then it is the sole information used to predict mortality rate. However, if longevity is not available, the model reverts to predicting mortality from growth parameters.

We then fit this model using phylogenetic structural equation models. We specifically apply a grid-search across the eight models formed by any combination of modeled transformations of the phylogenetic tree. We then use marginal AIC to select a model, and list estimated path coefficients.

```

# Specify SEM structure
sem_structure = "
  logK -> logtmax, b1
  logLinf -> logtmax, b2
  logtmax -> logM, a
"

# Grid-search model selection using AIC for transformations
Grid = expand.grid( "OU" = c(FALSE,TRUE),
                  "lambda" = c(FALSE,TRUE),
                  "kappa" = c(FALSE,TRUE) )

psem_grid = NULL
for( i in 1:nrow(Grid)){
  psem_grid[[i]] = phylosem( data=Data,
                           tree = tree,
                           sem = sem_structure,
                           estimate_ou = Grid[i,'OU'],
                           estimate_lambda = Grid[i,'lambda'],
                           estimate_kappa = Grid[i,'kappa'],
                           quiet = TRUE )
}

# Extract AIC for each model and rank-order by parsimony
Grid$AIC = sapply( psem_grid, \(m) m$opt$AIC )
Grid = Grid[order(Grid$AIC,decreasing=FALSE),]

```

```
# Select model with lowest AIC
psem_best = psem_grid[[as.numeric(rownames(Grid[1,]))]]
```

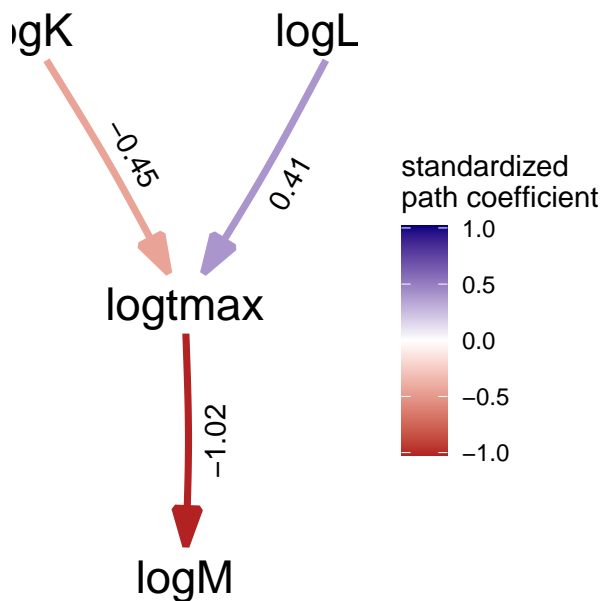
OU	lambda	kappa	AIC
FALSE	TRUE	TRUE	1552.940
FALSE	TRUE	FALSE	1553.164
TRUE	TRUE	TRUE	1559.502
TRUE	FALSE	TRUE	1561.424
TRUE	TRUE	FALSE	1563.372
FALSE	FALSE	TRUE	1643.863
TRUE	FALSE	FALSE	1717.509
FALSE	FALSE	FALSE	2358.137

Path	VarName	Estimate	StdErr	t.value	p.value
NA	Intercept_logM	1.668	0.318	5.250	0.000
NA	Intercept_logK	-1.759	0.566	3.107	0.002
NA	Intercept_logtmax	-0.575	0.655	0.878	0.380
NA	Intercept_logLinf	6.559	0.445	14.742	0.000
logK -> logtmax	b1	-0.448	0.067	6.716	0.000
logLinf -> logtmax	b2	0.407	0.086	4.731	0.000
logtmax -> logM	a	-1.022	0.037	27.732	0.000
logM <-> logM	V[logM]	0.056	0.014	3.966	0.000
logK <-> logK	V[logK]	0.105	0.026	4.047	0.000
logtmax <-> logtmax	V[logtmax]	0.078	0.019	4.029	0.000
logLinf <-> logLinf	V[logLinf]	0.082	0.020	4.122	0.000

Visualizing output

Finally, we can convert output to formats from other packages, and use existing and third-party PCM packages to plot, query, and post-process output.

```
# Plot path diagram
my_fitted_DAG = as_fitted_DAG(psem_best)
plot(my_fitted_DAG, type="color")
```



```

# Total, direct, and indirect effects
my_sem = as_sem(psem_best)
effects(my_sem)
#>
#> Total Effects (column on row)
#>      logK  logtmax  logLinf
#> logtmax -0.4480233  0.000000  0.4073488
#> logM     0.4579994 -1.022267 -0.4164192
#>
#> Direct Effects
#>      logK  logtmax  logLinf
#> logtmax -0.4480233  0.000000  0.4073488
#> logM     0.0000000 -1.022267  0.0000000
#>
#> Indirect Effects
#>      logK logtmax  logLinf
#> logtmax 0.0000000    0  0.0000000
#> logM    0.4579994    0 -0.4164192

```

We also show how to plot output using phylosignal, although it is currently unavailable on CRAN and therefore commented out:

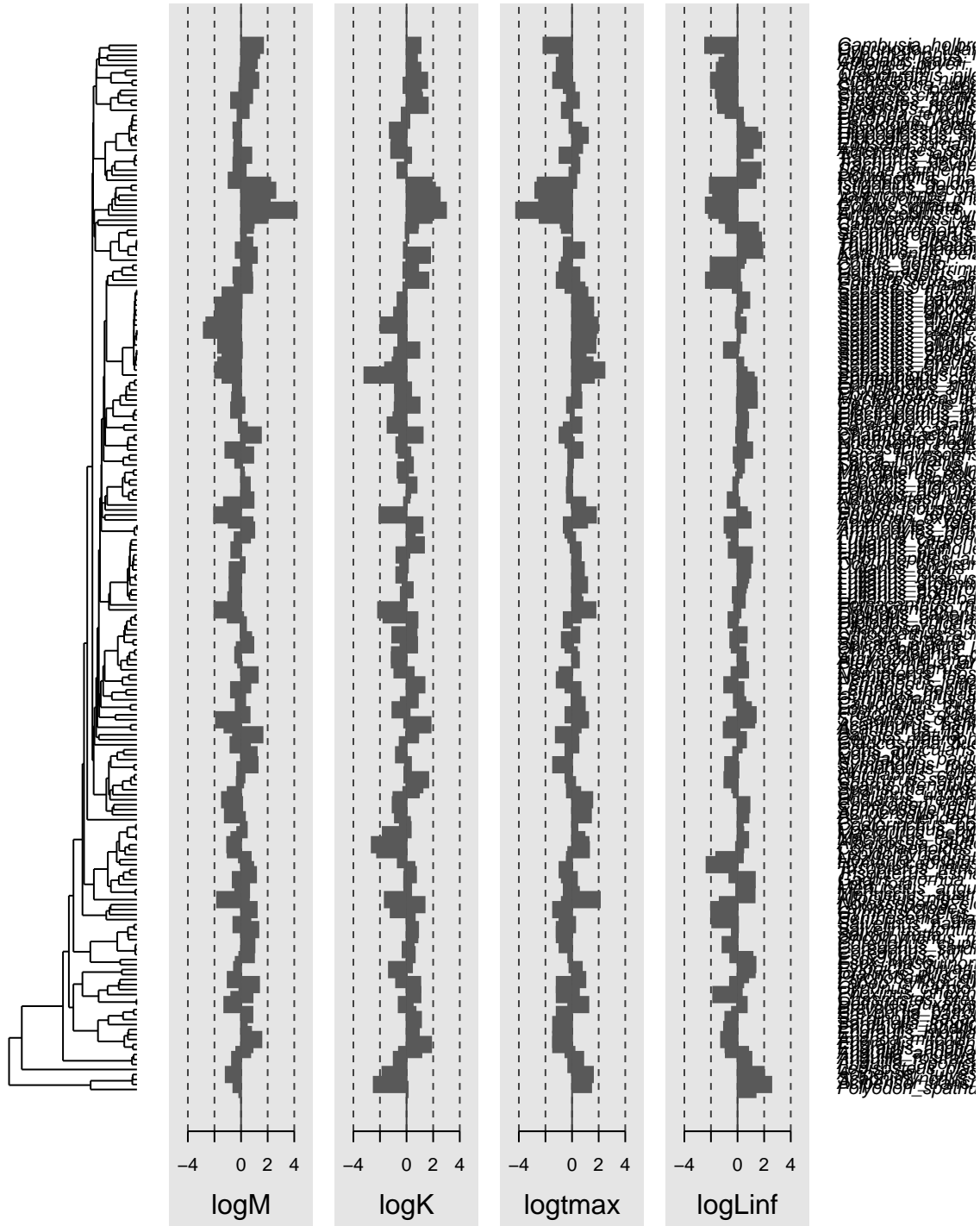
```

# Load for plotting,
# https://r-pkgs.org/vignettes.html#sec-vignettes-eval-option
library(phylosignal)

# Plot using phylobase
my_phylo4d = as_phylo4d( psem_best )

```

```
barplot(my_phylo4d)
```



Sensitivity to using taxonomic tree

After analysis, we can also conduct sensitivity analyses. Here, we show how to construct a taxonomic tree and use this in place of phylogenetic information. As before, this requires some code to reformat the data and then the statistical analysis is simple to specify. The estimated path coefficients are very similar to estimates when using phylogeny.

```
library(ape)
Data = Mlifehist_ver1_0

# Make taxonomic factors
Data$Genus_species = factor( paste0(Data$Genus, "_", Data$Species) )
Data$Genus = factor( Data$Genus )
Data$Family = factor( Data$Family )
Data$Order = factor( Data$Order )

# Make taxonomic tree
tree = ape::as.phylo( ~Order/Family/Genus/Genus_species, data=Data, collapse=FALSE)
tree$edge.length = rep(1,nrow(tree$edge))
tree = collapse.singles(tree)
tmp = root(tree, node=ape::Ntip(tree)+1 )

# Drop duplicates ... not dealing with variation among stocks within species
Data = Data[match(unique(Data$Genus_species),Data$Genus_species), ]

# log-transform to simplify later syntax
Data = cbind( Data, "logM" = log(Data[, 'M']),
              "logK" = log(Data[, 'K']),
              "logtmax" = log(Data[, 'tmax']),
              "logLinf" = log(Data[, 'Linf']) )

# Only include modeled variables in trait-data passed to phylosem
rownames(Data) = Data$Genus_species
Data = Data[,c('logM', 'logK', 'logtmax', 'logLinf')]

# Fit model
psem_taxon = phylosem( data=Data,
                      tree = tree,
                      sem = sem_structure,
                      estimate_ou = TRUE,
                      quiet = TRUE )

# Plot path diagram
my_fitted_DAG = as_fitted_DAG(psem_taxon)
plot(my_fitted_DAG, type="color")
```

