

Stability properties for MAR(1) models

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Background

There is growing interest in the use of first-order vector autoregressive models in ecology where they are often referred to as multivariate autoregressive, or MAR(1), models (*e.g.*, Ives *et al.* 2003 *Ecological Monographs* 73:301–330). In particular, MAR(1) models have been used to estimate interactions among various members in a food web and evaluate overall community stability.

The general form of a MAR(1) model is

$$\mathbf{x}_t = \mathbf{B}\mathbf{x}_{t-1} + \mathbf{w}_t, \quad (1)$$

where \mathbf{x}_t is an $n \times 1$ vector of state variates at time t , \mathbf{B} is an $n \times n$ transition matrix, and \mathbf{w}_t is an $n \times 1$ vector of multivariate normal process errors; $\mathbf{w}_t \sim \text{MVN}(\mathbf{0}, \mathbf{Q})$.

State-space model

This MAR(1) model can also be used as part of a state-space model, wherein the observed data \mathbf{y} are an imperfect sample of the true realizations \mathbf{x} , such that

$$\mathbf{y}_t = \mathbf{x}_t + \mathbf{v}_t \quad (2)$$

and \mathbf{v}_t is an $n \times 1$ vector of observation errors. When combined, Eqns (1) and (2) form a state-space model:

$$\begin{aligned} \mathbf{x}_t &= \mathbf{B}\mathbf{x}_{t-1} + \mathbf{w}_t \\ \mathbf{y}_t &= \mathbf{x}_t + \mathbf{v}_t \end{aligned} \quad (3)$$

Following Holmes *et al.* (2012 *The R Journal* 4:11-19), I will refer to this form of the MAR(1) model as a MARSS model, where SS stands for state-space, and we drop the parenthetic lag-1 identifier for convenience.

Non-zero mean in the observation

As defined here, the mean of both \mathbf{x} and \mathbf{y} is $\mathbf{0}$ for all t . If instead the mean of \mathbf{y} was non-zero, we could simply subtract the mean of the observations *a priori*. Thus, if we define \mathbf{a} to be an $n \times 1$ vector wherein the i -th element a_i is the mean of y_i , and $\mathbf{y}_t^* = \mathbf{y}_t - \mathbf{a}$, then the observation model becomes

$$\begin{aligned}
\mathbf{y}_t^* &= \mathbf{x}_t + \mathbf{v}_t \\
\mathbf{y}_t - \mathbf{a} &= \mathbf{x}_t + \mathbf{v}_t \\
\mathbf{y}_t &= \mathbf{x}_t + \mathbf{a} + \mathbf{v}_t
\end{aligned} \tag{4}$$

When Eqn (1) is combined with Eqn (4), the full state-space model becomes

$$\begin{aligned}
\mathbf{x}_t &= \mathbf{B}\mathbf{x}_{t-1} + \mathbf{w}_t \\
\mathbf{y}_t &= \mathbf{x}_t + \mathbf{a} + \mathbf{v}_t.
\end{aligned} \tag{5}$$

Non-zero mean in the state

Alternatively, we could instead specify the mean in the state model, such that if \mathbf{a} is an $n \times 1$ vector wherein the i -th element a_i is the mean of x_i , and $\mathbf{x}_t^* = \mathbf{x}_t - \mathbf{a}$, then the state model would be

$$\begin{aligned}
\mathbf{x}_t^* &= \mathbf{B}\mathbf{x}_{t-1}^* + \mathbf{w}_t \\
\mathbf{x}_t - \mathbf{a} &= \mathbf{B}(\mathbf{x}_{t-1} - \mathbf{a}) + \mathbf{w}_t \\
\mathbf{x}_t &= \mathbf{a} + \mathbf{B}(\mathbf{x}_{t-1} - \mathbf{a}) + \mathbf{w}_t
\end{aligned} \tag{6}$$

Combining Eqn (6) and Eqn (2) leads to this state-space model:

$$\begin{aligned}
\mathbf{x}_t &= \mathbf{a} + \mathbf{B}(\mathbf{x}_{t-1} - \mathbf{a}) + \mathbf{w}_t \\
\mathbf{y}_t &= \mathbf{x}_t + \mathbf{v}_t.
\end{aligned} \tag{7}$$

Importantly, both of the specifications of the MARSS models in Eqns (5) and (7) are equivalent, such that we would recover the same parameter values when estimated from the same data.

Effects of covariates

Often we would like to examine the potential effects of external drivers (covariates) on community dynamics (*e.g.*, temperature effects on poikilotherms),

Covariates in the state I

Traditionally, a MARSS model with covariate effects on the state is defined as

$$\begin{aligned}
\mathbf{x}_t &= \mathbf{B}\mathbf{x}_{t-1} + \mathbf{C}\mathbf{c}_t + \mathbf{w}_t \\
\mathbf{y}_t &= \mathbf{x}_t + \mathbf{v}_t
\end{aligned} \tag{8}$$

where \mathbf{C} is an $n \times p$ matrix of covariate effects, and \mathbf{c}_t is a $p \times 1$ vector of mean-zero covariates at time t .

However, when the state part of MARSS model is defined this way, the estimated covariate effects in $\hat{\mathbf{C}}$ will not reflect the true relationship between \mathbf{x} and \mathbf{c} . That is, if we regressed covariate c_j against

x_i , the absolute value of the estimated slope of the relationship would be larger than that for the i_j -th element of $\hat{\mathbf{C}}$.

We can demonstrate this phenomenon easily by obtaining realizations of the state model in Eqn (8). To keep things relatively simple, we will simulate interactions between wolves and moose, and assume there is one covariate (*e.g.*, temperature) that has positive, but different effects on each species. We will use a sine wave as a dummy covariate. Here is our process model

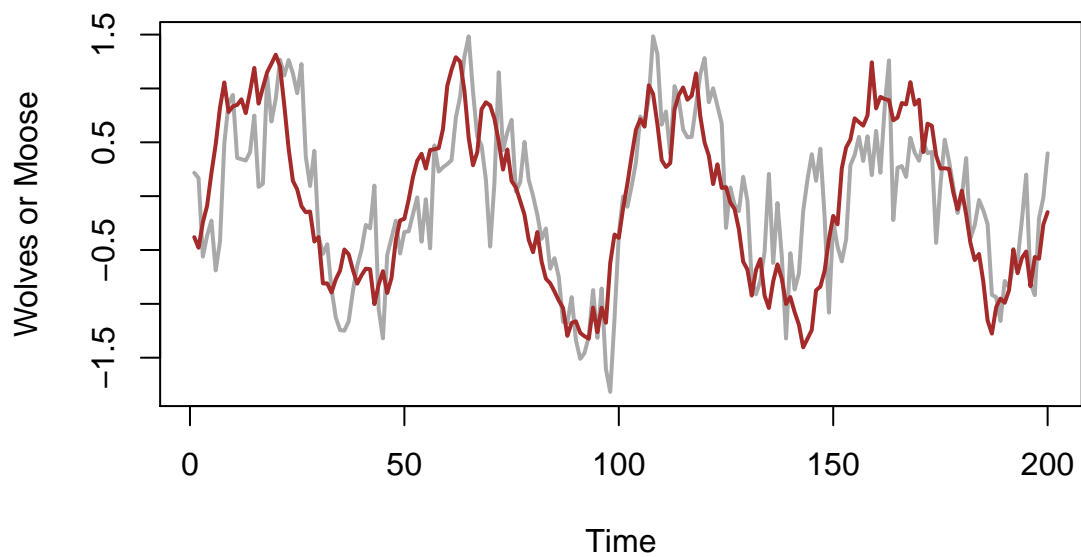
$$\begin{bmatrix} x_{wolves} \\ x_{moose} \end{bmatrix}_t = \begin{bmatrix} 0.6 & 0.2 \\ -0.1 & 0.8 \end{bmatrix} \begin{bmatrix} x_{wolves} \\ x_{moose} \end{bmatrix}_{t-1} + \begin{bmatrix} 0.1 \\ 0.3 \end{bmatrix} [c]_{t-1} + \begin{bmatrix} w_{wolves} \\ w_{moose} \end{bmatrix}_t. \quad (9)$$

We will further assume the process errors \mathbf{w}_t have different variances and zero covariance, such that.

$$\begin{bmatrix} w_{wolves} \\ w_{moose} \end{bmatrix}_t \sim \text{MVN} \left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} 0.03 & 0 \\ 0 & 0.15 \end{bmatrix} \right). \quad (10)$$

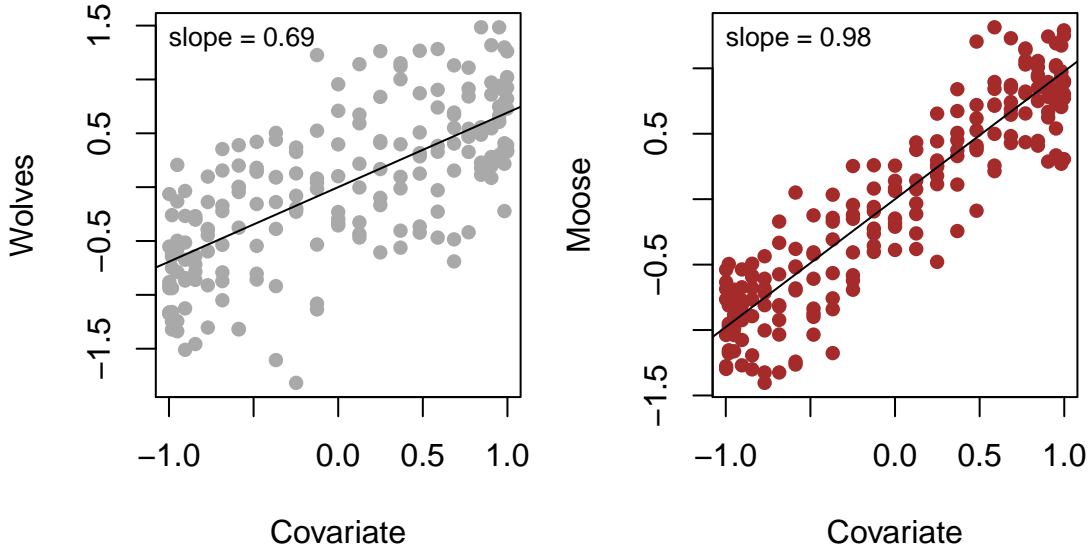
We begin by simulating 100 time steps from the model and plotting the time series for wolves (gray) and moose (brown).

```
library(MASS)
set.seed(123)
## time steps
TT <- 200
## interaction matrix
BB <- matrix(c(0.6,-0.1,0.2,0.8),2,2)
## covariate effects
CC <- matrix(c(0.1,0.3),2,1)
## dummy sinusoidal covariate
cc <- matrix(sin(2*pi*seq(TT)/50),1,TT)
## process variance
QQ <- matrix(c(0.15,0,0,0.03),2,2)
## process errors
xx <- ww <- t(mvrnorm(TT, matrix(c(0,0),2,1), QQ))
## simulate process
for(t in 2:TT) {
  xx[,t] <- BB %*% xx[,t-1] + CC %*% cc[,t,drop=FALSE] + ww[,t]
}
## plot states
par(mai=c(0.8,0.8,0.2,0.2), omi=c(0.5,0.1,0.5,0.1))
plot.ts(xx[1,], ylab="Wolves or Moose", col="darkgray", ylim=c(min(xx), max(xx)), lwd=2)
lines(xx[2,], col="brown", lwd=2)
```



Now we can examine the relationship between **x** and **c**.

```
## slopes
sw <- coef(lm(xx[1,] ~ cc[1,] - 1))
sm <- coef(lm(xx[2,] ~ cc[1,] - 1))
## plot covariate vs states
par(mfrow=c(1,2), mai=c(0.8,0.8,0.2,0.2), oma=c(0.5,0.1,0.5,0.1))
plot(cc, xx[1,], pch=16, ylab="Wolves", xlab="Covariate", col="darkgray")
abline(a=0, b=sw)
text(-1, max(xx[1,]), substitute(paste("slope = ", s), list(s = round(sw, 2))),
      adj=c(0,1), cex=0.8)
plot(cc, xx[2,], pch=16, ylab="Moose", xlab="Covariate", col="brown")
abline(a=0, b=sm)
text(-1, max(xx[2,]), substitute(paste("slope = ", s), list(s = round(sm, 2))),
      adj=c(0,1), cex=0.8)
```



From these results we can clearly see that the expected relationships between the states and covariate do not hold and that they are indeed biased high.

Covariates in the state II

Based on the formulation of the state model in Eqn (6), we can instead replace the specific mean vector \mathbf{a} with a general term for the expectation of \mathbf{x} at time t , $E(\mathbf{x}_t)$, such that

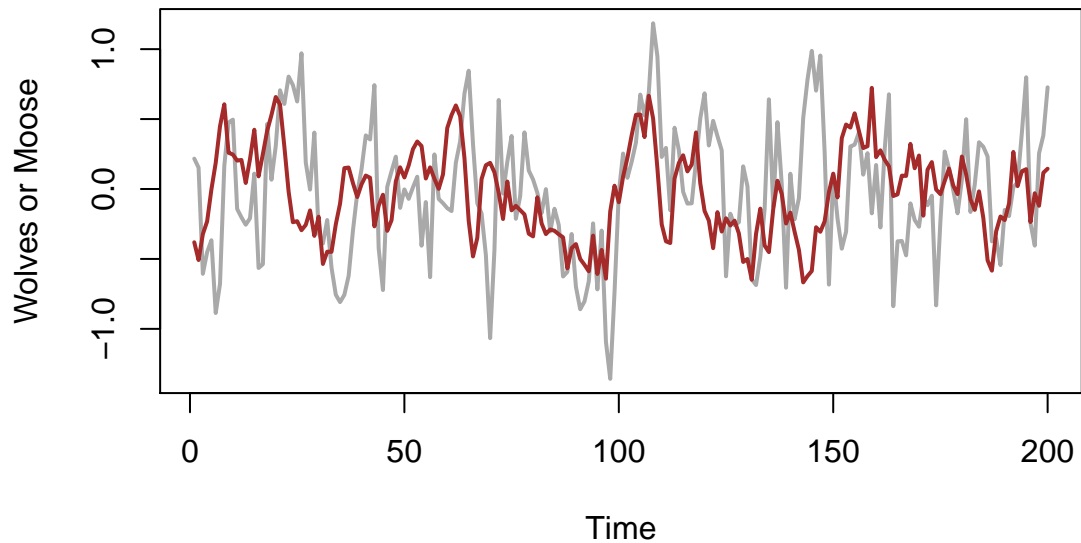
$$\mathbf{x}_t = E(\mathbf{x}_t) + \mathbf{B}(\mathbf{x}_{t-1} - E(\mathbf{x}_{t-1})) + \mathbf{w}_t. \quad (11)$$

At this point we are making no assumptions about the underlying factors that contribute to $E(\mathbf{x}_t)$, in that there could be some underlying mean, trend, or periodicity in the state. Thus, in a model with covariate effects on the state, we would write the state-space model as

$$\begin{aligned} \mathbf{x}_t &= \mathbf{C}\mathbf{c}_t + \mathbf{B}(\mathbf{x}_{t-1} - \mathbf{C}\mathbf{c}_{t-1}) + \mathbf{w}_t \\ \mathbf{y}_t &= \mathbf{x}_t + \mathbf{v}_t. \end{aligned} \quad (12)$$

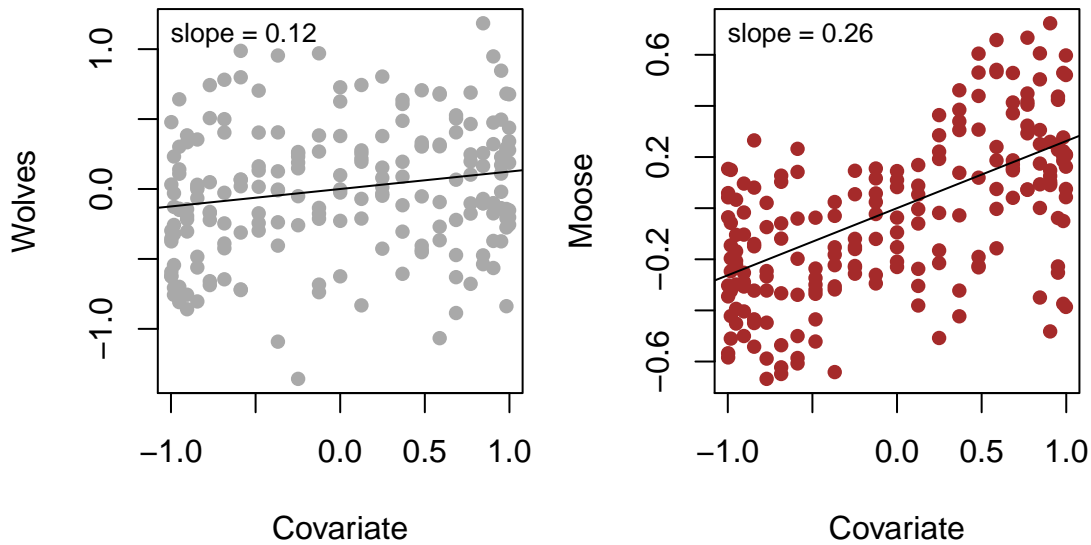
We can now simulate from Eqn (12) and again examine the relationship between \mathbf{x} and \mathbf{c} under this new formulation.

```
## simulate process
for(t in 2:TT) {
  xx[,t] <- BB %*% (xx[,t-1] - CC %*% cc[,t-1]) + CC %*% cc[,t] + ww[,t]
}
## plot states
par(mai=c(0.8,0.8,0.2,0.2), oma=c(0.5,0.1,0.5,0.1))
plot.ts(xx[1,], ylab="Wolves or Moose", col="darkgray", ylim=c(min(xx), max(xx)), lwd=2)
lines(xx[2,], col="brown", lwd=2)
```



And now we can again examine the estimated relationship between **c** and **x**.

```
## slopes
sw <- coef(lm(xx[1,] ~ cc[1,] - 1))
sm <- coef(lm(xx[2,] ~ cc[1,] - 1))
## plot covariate vs states
par(mfrow=c(1,2), mai=c(0.8,0.8,0.2,0.2), omi=c(0.5,0.1,0.5,0.1))
plot(cc, xx[1,], pch=16, ylab="Wolves", xlab="Covariate", col="darkgray")
abline(a=0, b=sw)
text(-1, max(xx[1,]), substitute(paste("slope = ", s), list(s = round(sw, 2))),
      adj=c(0,1), cex=0.8)
plot(cc, xx[2,], pch=16, ylab="Moose", xlab="Covariate", col="brown")
abline(a=0, b=sm)
text(-1, max(xx[2,]), substitute(paste("slope = ", s), list(s = round(sm, 2))),
      adj=c(0,1), cex=0.8)
```



Here we can see that the estimated relationships between the covariate and the states are much closer to their true values.

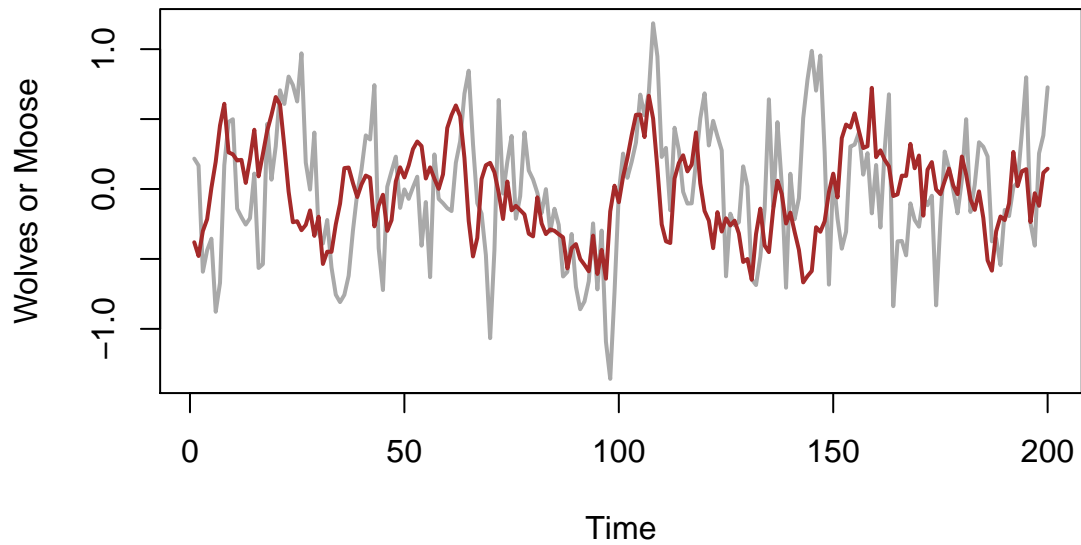
Covariates in the observation

We saw previously how to include a non-zero mean in the observation model, which was equivalent to doing so in the state model. The same reasoning applies here with respect to covariates in the observation. Using the relationship above in Eqn (4), we can write the state-space model as

$$\begin{aligned} \mathbf{x}_t &= \mathbf{B}\mathbf{x}_{t-1} + \mathbf{w}_t \\ \mathbf{y}_t &= \mathbf{x}_t + \mathbf{C}\mathbf{c}_t + \mathbf{v}_t. \end{aligned} \quad (13)$$

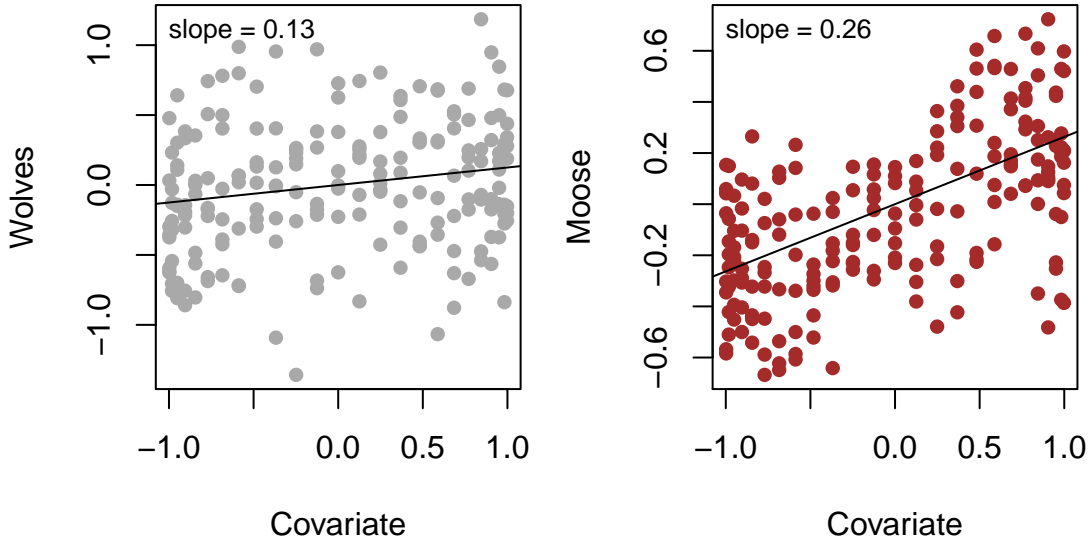
As before, we can simulate some data from this model and examine the relationships between \mathbf{c} and the observed data \mathbf{y} . To keep the comparison the same as before, we will assume that there is no observation error (*i.e.*, $\mathbf{v}_t = 0 \forall t$).

```
## initialize y
yy <- xx
## simulate data
for(t in 2:TT) {
  xx[,t] <- BB %*% xx[,t-1] + ww[,t]
  yy[,t] <- xx[,t] + CC %*% cc[,t]
}
## plot states
par(mai=c(0.8,0.8,0.2,0.2), omi=c(0.5,0.1,0.5,0.1))
plot.ts(yy[1,], ylab="Wolves or Moose", col="darkgray", ylim=c(min(yy), max(yy)), lwd=2)
lines(yy[2,], col="brown", lwd=2)
```



And lastly we can examine the estimated relationship between `c` and `y`.

```
## slopes
sw <- coef(lm(yy[1,] ~ cc[1,] - 1))
sm <- coef(lm(yy[2,] ~ cc[1,] - 1))
## plot covariate vs states
par(mfrow=c(1,2), mai=c(0.8,0.8,0.2,0.2), omi=c(0.5,0.1,0.5,0.1))
plot(cc, yy[1,], pch=16, ylab="Wolves", xlab="Covariate", col="darkgray")
abline(a=0, b=sw)
text(-1, max(yy[1,]), substitute(paste("slope = ", s), list(s = round(sw, 2))),
      adj=c(0,1), cex=0.8)
plot(cc, yy[2,], pch=16, ylab="Moose", xlab="Covariate", col="brown")
abline(a=0, b=sm)
text(-1, max(yy[2,]), substitute(paste("slope = ", s), list(s = round(sm, 2))),
      adj=c(0,1), cex=0.8)
```

Again, the estimated relationships are the same as before.

Variance of the stationary distribution

We will restrict this treatment to stationary models wherein all of the eigenvalues of \mathbf{B} lie within the unit circle. Because $t = (t - 1)$ as $t \rightarrow \infty$, under assumptions of stationarity we can write the process equation from the above state-space model as

$$\mathbf{x}_t = \mathbf{B}\mathbf{x}_t + \mathbf{w}_t.$$

From this, it follows that

$$\text{Var}(\mathbf{x}_t) = \mathbf{B}\text{Var}(\mathbf{x}_t)\mathbf{B}^\top + \text{Var}(\mathbf{w}_t).$$

If we define $\Sigma = \text{Var}(\mathbf{x}_t)$, then

$$\Sigma = \mathbf{B}\Sigma\mathbf{B}^\top + \mathbf{Q}.$$

Unfortunately, there is no closed-form solution for Σ when written in this form. However, we can use the vec operator to derive an explicit solution for Σ . The vec operator converts an $i \times j$ matrix into an $(ij) \times 1$ column vector. For example, if

$$\mathbf{M} = \begin{bmatrix} 1 & 3 \\ 2 & 4 \end{bmatrix},$$

then

$$\text{vec}(\mathbf{M}) = \begin{bmatrix} 1 \\ 2 \\ 3 \\ 4 \end{bmatrix}.$$

Thus, if \mathbf{I} is an $n \times n$ identity matrix, and we define $\mathcal{I} = \mathbf{I} \otimes \mathbf{I}$ and $\mathcal{B} = \mathbf{B} \otimes \mathbf{B}$, then

$$\text{vec}(\mathbf{\Sigma}) = (\mathcal{I} - \mathcal{B})^{-1} \text{vec}(\mathbf{Q}).$$

Importance of species interactions to stability

Among the many ways of classifying stability, I am interested in the extent to which community interactions, relative to environmental forcing, contribute to the overall variance of the stationary distribution. In a stable system, any perturbation affecting one or more of the community members does not amplify as it moves throughout the community as a whole, such that the variances in log-densities over time would be driven almost entirely by random environmental variation. Given that same magnitude of random environmental variation, less stable systems are characterized by greater variances in the temporal dynamics of their constituents.

Here we will use determinants to measure the “volume” of a matrix. Looking back to the matrix form of the equation for the variance of the stationary distribution, we see that

$$\mathbf{\Sigma} = \mathbf{B}\mathbf{\Sigma}\mathbf{B}^\top + \mathbf{Q},$$

and hence

$$\mathbf{\Sigma} - \mathbf{Q} = \mathbf{B}\mathbf{\Sigma}\mathbf{B}^\top.$$

Therefore, the volume of the difference $\mathbf{\Sigma} - \mathbf{Q}$ provides a measure of how much species interactions contribute to the variance of the stationary distribution. Taking determinants of both sides, we get

$$\begin{aligned} \det(\mathbf{\Sigma} - \mathbf{Q}) &= \det(\mathbf{B}\mathbf{\Sigma}\mathbf{B}^\top) \\ &= \det(\mathbf{B})\det(\mathbf{\Sigma})\det(\mathbf{B}^\top) \\ &= \det(\mathbf{B})\det(\mathbf{\Sigma})\det(\mathbf{B}). \end{aligned}$$

The proportion $\pi_{\mathbf{B}}$ of the volume of $\mathbf{\Sigma}$ attributable to species interactions is then

$$\pi_{\mathbf{B}} = \frac{\det(\mathbf{\Sigma} - \mathbf{Q})}{\det(\mathbf{\Sigma})} = \det(\mathbf{B})^2.$$

The effects of covariates

Often we would like to examine the potential effects of covariates on community dynamics. In that case, the MARSS(1) model becomes

$$\begin{aligned}\mathbf{x}_t &= \mathbf{B}\mathbf{x}_{t-1} + \mathbf{C}\mathbf{c}_t + \mathbf{w}_t, \\ \mathbf{y}_t &= \mathbf{x}_t + \mathbf{a} + \mathbf{v}_t,\end{aligned}$$

where \mathbf{C} is an $n \times p$ matrix of covariate effects, and \mathbf{c}_t is a $p \times 1$ vector of covariates at time t . Although the variance of the stationary distribution will be affected by any covariate effects, the method described above for estimating the relative effects of species interactions is unaffected. That is, if $\mathbf{\Xi}$ is the variance-covariance matrix of the covariates in \mathbf{c} , then analogous to above the variance of the stationary distribution will be

$$\begin{aligned}\mathbf{\Sigma} &= \mathbf{B}\mathbf{\Sigma}\mathbf{B}^\top + \mathbf{C}\mathbf{\Xi}\mathbf{C}^\top + \mathbf{Q}, \\ \mathbf{\Sigma} - \mathbf{C}\mathbf{\Xi}\mathbf{C}^\top - \mathbf{Q} &= \mathbf{B}\mathbf{\Sigma}\mathbf{B}^\top,\end{aligned}$$

and hence the proportion $\pi_{\mathbf{B}}$ of the volume of $\mathbf{\Sigma}$ attributable to species interactions is, as before, given by

$$\pi_{\mathbf{B}} = \frac{\det(\mathbf{\Sigma} - \mathbf{C}\mathbf{\Xi}\mathbf{C}^\top - \mathbf{Q})}{\det(\mathbf{\Sigma})} = \det(\mathbf{B})^2.$$

Long-term changes in abundance

Ives *et al.* (*Ecology* 1999 80:1405–1421) provide a means for assessing the expected long-term change in the density (biomass) of species i , L_i , within a community of p total members, owing to the effect of some covariate j . Specifically,

$$L_i = \frac{\det(\mathbf{B}_1 \ \dots \ \mathbf{B}_{i-1} \ \mathbf{C}_j \ \mathbf{B}_{i+1} \ \dots \ \mathbf{B}_p)}{\det(\mathbf{B}_1 \ \dots \ \mathbf{B}_p)},$$

where \mathbf{B}_i is a $p \times 1$ column vector containing the estimated effects of species i on all of the species (including itself), and \mathbf{C}_i is a $p \times 1$ column vector containing the estimated effects of covariate j on each of the species.

Reactivity

We can also calculate the reactivity of a community following an external perturbation, which measures the displacement of the community away from its stationary distribution. There are two methods to do so.

The first follows Ives *et al.* (2003), where reactivity is based upon estimates of the process covariance \mathbf{Q} and stationary covariance $\mathbf{\Sigma}$. Specifically, they define reactivity as

$$-\frac{\text{tr}(\mathbf{Q})}{\text{tr}(\mathbf{\Sigma})} \leq 1 - \lambda_{max}(\mathbf{B}^\top \mathbf{B}).$$

The second method comes from Neubert *et al.* (2009), wherein reactivity is

$$\log \|\mathbf{B}\|_2 = \log \sqrt{\lambda_{max}(\mathbf{B}^\top \mathbf{B})} = \log \sigma_{max}(\mathbf{B}),$$

and $\|\cdot\|_2$ is the spectral norm, $\lambda_{max}(\cdot)$ is the maximum eigenvalue, and $\sigma_{max}(\cdot)$ is the largest singular value. This method only requires estimates of the species interactions in \mathbf{B} .

Effect of density-dependence

In a MAR(1) model of community dynamics, the matrix \mathbf{B} maps the vector of log-densities from one time step to another. In particular, the diagonal elements of \mathbf{B} control the degree of density-dependence via the degree of so-called mean reversion. Because we are interested in stationary dynamics, the diagonals of \mathbf{B} will all be less than 1 in absolute value. As such, here are a few generalizations:

1. As $|b_{ii}| \rightarrow 0$ the strength of density dependence increases (*i.e.*, the degree of mean reversion increases);
2. As $b_{ii} \rightarrow 1$ the strength of density dependence decreases to the point where there is no density dependence when $b_{ii} = 1$ (*i.e.*, the temporal dynamics become a non-stationary random walk); and

Furthermore, the determinant (and the trace) of a matrix are functions of the eigenvalues λ_i , such that for an $N \times N$ matrix \mathbf{B} :

$$\det(\mathbf{B}) = \prod_{i=1}^N \lambda_i.$$

The eigenvalues themselves are a function of all of the elements in \mathbf{B} , but they are particularly sensitive to the elements along the diagonal. We can formally examine the sensitivity of $\det(\mathbf{B})$ to each of the elements in \mathbf{B} via the following relationship:

$$\frac{\partial \det(\mathbf{B})}{\partial \mathbf{B}_{ij}} = \det(\mathbf{B})(\mathbf{B}^{-1})_{ji}.$$

Thus, for any matrix \mathbf{B} we can ask whether its determinant is most sensitive to a diagonal versus an off-diagonal element.