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Introduction

This is a reproduction of the analyses presented in the paper *Chaos in a long-term experiment with a plankton community*, by Elisa Benincà and others ([the paper on the Nature website](#)). Details of the methods are in [the Supplement to the Nature paper](#).

This reproduction was made as part of the Reproducible Research in Ecology, Evolution, Behaviour, and Environmental Studies (RREEBES) Course, lead by Owen Petchey at the University of Zurich. More information about the course [here](#) on github.

The code and data for the reproduction are [here](#) on github.

Authors

Lead author was Owen Petchey. Frank Pennekamp and Marco Plebani made sizeable contributions. All contributors are detailed on github in the commit history etc.

Known issues

The known issues / problems with this reproduction are with the prefix “Beninca” [here](#). Please add and or solve issues there.

The data

The data are available as an Excel file supplement to [an Ecology Letters publication](#). The Excel file contains several datasheets. Two are particularly important, as they are the source of the raw data (one contains original species abundances, the one with the nutrient concentrations). Another datasheet in the ELE supplement contains transformed variables. We also got some data direct from Steve Ellner, see below for details.

In the code below, the data and any other files are read from github, which means there must be a connection to github.

First get the raw data into R and tidy it.

All required libraries:

```
rm(list=ls())
library(tidyr)
library(dplyr)
library(lubridate)
library(stringr)
library(ggplot2)
library(RCurl)
library(pracma)
library(oce)
library(tseriesChaos)
library(reshape2)
library(mgcv)
```

```
library(repmis)

spp.abund <- read.csv(text=getURL("https://raw.githubusercontent.com/opetchey/RREEBES/master/Beninca_et"))

spp.abund <- select(spp.abund, -X, -X.1)
spp.abund <- spp.abund[-804:-920,]
str(spp.abund)

## 'data.frame': 803 obs. of 12 variables:
## $ Date : Factor w/ 803 levels "", "01/02/91",...: 306 440 465 498 520 601 628 673 699 7
## $ Day.number : int 1 6 7 8 9 12 13 15 16 19 ...
## $ Cyclopoids : num 0 0 0.0353 0 0.0353 ...
## $ Calanoid.copepods : num 1.04 2.03 1.72 2.41 1.71 ...
## $ Rotifers : num 7.7 10.19 8.08 6.06 5.94 ...
## $ Protozoa : Factor w/ 330 levels "", "0", "0,000001",...: 1 1 1 1 1 1 1 1 1 1 ...
## $ Nanophytoplankton : num 0.106 0.212 0.212 0.212 0.212 ...
## $ Picophytoplankton : num 1 2 1.52 1.52 1.98 ...
## $ Filamentous.diatoms: num 0 0 0 0 0 0 0 0 0 0 ...
## $ Ostracods : num 0 0 0 0.0187 0 ...
## $ Harpacticoids : num 0 0 0 0 0 0 0 0 0 0 ...
## $ Bacteria : num 2.15 1.97 1.79 1.61 1.43 ...
```

The Protozoa variable contains some numbers with comma as the decimal separator. This creates a question about what dataset was used for the original analyses, as it could not have been this one.

```
spp.abund$Protozoa <- as.numeric(str_replace(spp.abund$Protozoa, ",", "."))
```

Format the dates as dates

```
spp.abund$Date <- dmy(spp.abund$Date)
```

Ooops... R assumes the experiment was done in the 21st century. Shouldn't matter too much.

Check dates match the Day.number (should give true):

```
sum(spp.abund$Day.number == 1+as.numeric((spp.abund$Date - spp.abund$Date[1]) / 24 / 60 / 60)) == length(spp.abund$Day.number)
```

```
## [1] TRUE
```

Check for duplicate dates:

```
spp.abund$Date[duplicated(spp.abund$Date)]
```

```
## [1] "2096-10-28 UTC"
```

```
which(duplicated(spp.abund$Date))
```

```
## [1] 702
```

Original dataset contains a duplicated date: 28/10/1996 (row 709 and 710 in excel sheet). Lets change the date in row 709 to 26/10/1996, which will put it half way between the two surrounding dates:

```
which(spp.abund$Date==ymd("2096-10-28 UTC"))
```

```
## [1] 701 702
```

```
spp.abund$Date[701] <- ymd("2096-10-26 UTC")
```

Check dates match the Day.number (should give true):

```
sum(spp.abund$Day.number == 1+as.numeric((spp.abund$Date - spp.abund$Date[1]) / 24 / 60 / 60)) == length(spp.abund$Day.number)
```

```
## [1] FALSE
```

Fix the Day.number problem:

```
spp.abund$Day.number <- 1+as.numeric((spp.abund$Date - spp.abund$Date[1]) / 24 / 60 / 60)
```

Data is in wide format, so change it to long:

```
spp.abund <- gather(spp.abund, "variable", "value", 3:12)
str(spp.abund)
```

```
## 'data.frame': 8030 obs. of 4 variables:
## $ Date : POSIXct, format: "2090-07-12" "2090-07-17" ...
## $ Day.number: num 1 6 7 8 9 12 13 15 16 19 ...
## $ variable : Factor w/ 10 levels "Cyclopoids","Calanoid.copepods",...: 1 1 1 1 1 1 1 1 1 1 ...
## $ value : num 0 0 0.0353 0 0.0353 ...
```

Bring in the nutrient data:

```
nuts <- read.csv(text=getURL("https://raw.githubusercontent.com/opetchey/RREEBES/master/Beninca_etal_2008_Nature/data/nutrients_origin.csv"))
#nuts <- read.csv("~/Dropbox (Dept of Geography)/RREEBES/Beninca_etal_2008_Nature/data/nutrients_origin.csv")

nuts <- select(nuts, -X, -X.1)
nuts <- nuts[-349:-8163,]
nuts$Date <- dmy(nuts$Date)
nuts <- select(nuts, -NO2, -NO3, -NH4)
#nuts$Date[duplicated(nuts$Date)]
#which(duplicated(nuts$Date))
nuts <- gather(nuts, "variable", "value", 3:4)
str(nuts)
```

```
## 'data.frame': 696 obs. of 4 variables:
## $ Date : POSIXct, format: "2090-09-18" "2090-09-24" ...
## $ Day.number: int 69 75 82 90 96 103 110 117 124 131 ...
## $ variable : Factor w/ 2 levels "Total.dissolved.inorganic.nitrogen",...: 1 1 1 1 1 1 1 1 1 1 ...
## $ value : num 28.32 20.84 11.15 15.5 5.92 ...
```

Now put the two datasets together

```
all.data <- rbind(spp.abund, nuts)
```

Now select only the date range used in the Nature paper. From the supplement *The analysis in Benincà et al. (Nature 2008)* covered all data from 16/06/1991 until 20/10/1997. (Remembering dates in the R dataframes are 2090s.)

```
all.data <- filter(all.data, Date>=dmy("15/06/2091") & Date<=dmy("21/10/2097"))

#all.data[all.data$Date==dmy("16/06/2091"),]
#all.data[all.data$Date==dmy("20/10/2097"),]
```

Reproducing figure 1b through 1g

(No attempt to reproduce Figure 1a, as its a food web diagram.)

First quick go:

Now we add a column that gives the variable types, same as in figure 1b through 1g. First make a lookup table giving species type:

```
tt <- data.frame(variable=unique(all.data$variable),
                 Type=c("Cyclopoids", "Herbivore", "Herbivore", "Herbivore",
                        "Phytoplankton", "Phytoplankton", "Phytoplankton",
                        "Detritivore", "Detritivore", "Bacteria", "Nutrient", "Nutrient"))
#tt
```

And add the Type variable to the new dataset:

```
all.data <- merge(all.data, tt)
```

First lets set the colours as in the original:

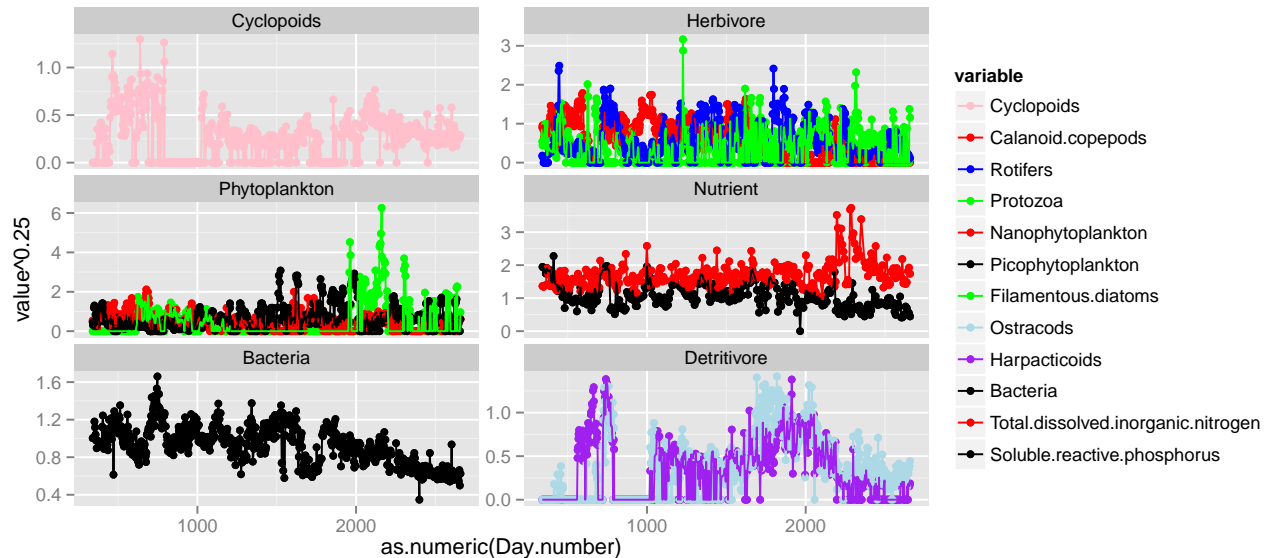
```
species.colour.mapping <- c("Cyclopoids"="pink",
                            "Calanoid.copepods"="red",
                            "Rotifers"="blue",
                            "Protozoa"="green",
                            "Nanophytoplankton"="red",
                            "Picophytoplankton"="black",
                            "Filamentous.diatoms"="green",
                            "Ostracods"="lightblue",
                            "Harpacticoids"="purple",
                            "Bacteria"="black",
                            "Total.dissolved.inorganic.nitrogen"="red",
                            "Soluble.reactive.phosphorus"="black")
```

Next change the order of the levels in the Type variable, so plots appear in the same order as in the original figure:

```
all.data$Type <- factor(all.data$Type, levels=c("Cyclopoids", "Herbivore", "Phytoplankton", "Nutrient",
                                                "Bacteria", "Detritivore"))
```

The graph with abundances fourth root transformed, as this is the transformation used in the ms.

```
g1 <- qplot(as.numeric(Day.number), value^0.25, col=variable, data=all.data) +
  facet_wrap(~Type, ncol=2, scales="free_y") +
  geom_point() + geom_line() +
  scale_colour_manual(values = species.colour.mapping)
g1
```



Data transformation

Now we need to work with transformed data. Details of the transformation, copied from the Supplementary information are in indented quote style in the following sections... looks like this:

3. Transformation of the time series. We transformed the original time series, shown in Fig. 1b-g of the main text, to obtain stationary time series with equidistant data and homogeneous units of measurement. The transformation steps are illustrated for the bacteria (Fig. S1).

Aside: The ELE supplement contains the raw data and the transformed data, in separate data sheets. I (Owen) also got the interpolated data from Stephen Ellner directly.

Interpolation

First, the time series were interpolated using cubic hermite interpolation, to obtain data with equidistant time intervals of 3.35 days (Fig. S1a).

Make a sequence of times at which to interpolate.

```
#aggregate(Day.number ~ variable, all.data, min)
#aggregate(Day.number ~ variable, all.data, max)
#xout <- seq(343.35, 2657.2, by=3.35)
xout <- seq(343.35, 2658, by=3.35)
#range(xout)
```

```

all.data1 <- na.omit(all.data)

#group_by(all.data1, variable) %>% summarise(out=min(Day.number))

mt <- plyr::dply(all.data1,
  "variable",
  function(xx) pracma::interp1(x=xx$Day.number,
    y=xx$value,
    xi=xout,
    method="cubic"))

## Aside: the duplicated date that was previously fixed was only discovered by a warning message
## given by the pracma::interp1 function!!!

mt <- as.data.frame(mt)
mt <- cbind(Day.number=xout, mt)
mt <- gather(mt, variable, value, 2:13)
#ggplot(mt, aes(x=Day.number, y=value)) + facet_wrap(~variable, scales="free") + geom_line()

```

Check this against the data direct from Steve:

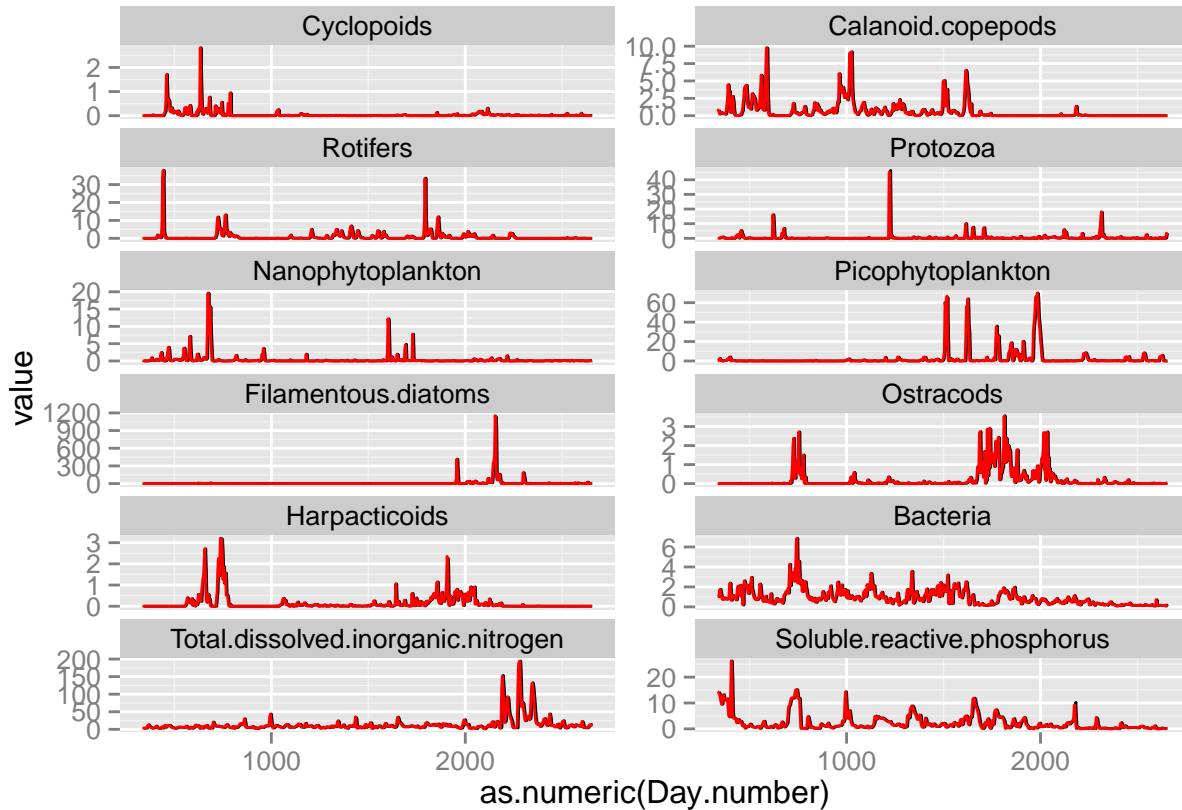
```

#from.steve <- read.csv("~/Dropbox (Dept of Geography)/RREEBES/Beninca_etal_2008_Nature/data/direct from
from.steve <- read.csv(text=getURL("https://raw.githubusercontent.com/opetchey/RREEBES/Beninca_developm
from.steve <- gather(from.steve, Species, Abundance, 2:13)

names(from.steve) <- c("Day.number", "variable", "value")

g1 <- ggplot(mt, aes(x=as.numeric(Day.number), y=value)) +
  facet_wrap(~variable, ncol=2, scales="free_y") +
  geom_line(size=0.5, col="black") +
  scale_colour_manual(values = species.colour.mapping)
g2 <- geom_line(data=from.steve, aes(x=Day.number, y=value), col="red")
g1 + g2

```



Looks very good.

Fourth root transform

Next, because the original time series showed many sharp spikes, the time series were rescaled using a fourth-root power transformation (Fig. S1b). The sharp spikes bias “direct method” estimates of the Lyapunov exponent, because nearby pairs of reconstructed state vectors mostly occurred in the troughs between spikes. The average rate of subsequent trajectory divergence from these pairs is therefore an estimate of the local Lyapunov exponent in the troughs, which may be very different from the global Lyapunov exponent. By making spikes and troughs more nearly symmetric, the power transformation resulted in a much more even spread of nearby state vector pairs across the full range of the data for all functional groups in the food web. The transformation is also useful for fitting nonlinear models of the deterministic skeleton (used for nonlinear predictability and indirect method estimates of the Lyapunov exponent), which was done by least squares and therefore is most efficient when error variances are stabilized. Fourth-root transformation is intermediate between the square-root transformation that would approximately stabilize the measurement error variance in count data from random subsamples, and the log transformation that is usually recommended for stabilizing process noise variance due to stochastic variation in birth and death rates.

```
mt$fr.value <- mt$value^0.25
```

Detrend

The time series were then detrended using a Gaussian kernel with a bandwidth of 300 days (red line in Fig. S1b), to obtain stationary time series. Most species did not show long-term

trends, except for the bacteria, detritivores (ostracods and harpacticoid copepods), dissolved inorganic nitrogen and soluble reactive phosphorus. One possible explanation for these trends in the microbial loop could be the slow accumulation of refractory organic material in the mesocosm, but we have not measured this component.

```
ww.td <- filter(mt, variable=="Total.dissolved.inorganic.nitrogen" |
                variable=="Soluble.reactive.phosphorus" |
                variable=="Bacteria" |
                variable=="Ostracods" |
                variable=="Harpacticoids")
## and to not detrend
ww.ntd <- filter(mt, variable!="Total.dissolved.inorganic.nitrogen" &
                variable!="Soluble.reactive.phosphorus" &
                variable!="Bacteria" &
                variable!="Ostracods" &
                variable!="Harpacticoids")
## detrend:
ww1 <- group_by(ww.td, variable) %>%
  mutate(trend=ksmooth(Day.number,fr.value,bandwidth=300,kernel="normal")$y)
ww1$dt.value <- ww1$fr.value-ww1$trend
#ww1 <- select(ww1, trend)

## don't detrend
ww2 <- ww.ntd
ww2$trend <- 0

ww2$dt.value <- ww2$fr.value

## rejoin
detrended <- rbind(ww1, ww2)
```

Rescale

Finally, the time series were linearly rescaled to have zero mean and a standard deviation of 1 (Fig. S1c).

(Note that this standardisation is not done in the code sent by Stephen. Probably shouldn't make a difference in the GAMs?)

```
## standardise
final <- group_by(detrended, variable) %>%
  mutate(stand.y=as.numeric(scale(dt.value)))
summarise(final, mean=mean(stand.y), sd=sd(stand.y))

## Source: local data frame [12 x 3]
##
##           variable      mean sd
## 1      Cyclopoids 9.634479e-17  1
## 2 Calanoid.copepods -1.095537e-16  1
## 3       Rotifers -1.713118e-17  1
## 4       Protozoa -4.973648e-17  1
## 5 Nanophytoplankton -1.962422e-17  1
```

```
## 6          Picophytoplankton  8.998258e-17  1
## 7      Filamentous.diatoms  1.560308e-18  1
## 8          Ostracods  1.247664e-17  1
## 9      Harpacticoids  2.274746e-17  1
## 10         Bacteria -2.289400e-17  1
## 11 Total.dissolved.inorganic.nitrogen -1.341386e-17  1
## 12      Soluble.reactive.phosphorus  2.788596e-17  1
```

```
## or don't standardise
#final <- detrended
final$y <- final$dt.value
summarise(final, mean=mean(y), sd=sd(y))
```

```
## Source: local data frame [12 x 3]
##
##           variable      mean      sd
## 1      Cyclopoids  0.2759440203  0.2238128
## 2  Calanoid.copepods  0.5529978074  0.4662991
## 3      Rotifers  0.5600824437  0.4515450
## 4      Protozoa  0.4328845135  0.4276168
## 5  Nanophytoplankton  0.4641707783  0.3351492
## 6      Picophytoplankton  0.6862112846  0.5691586
## 7  Filamentous.diatoms  0.4610865686  0.8332533
## 8      Ostracods -0.0005026064  0.2175769
## 9  Harpacticoids -0.0015090396  0.2147749
## 10         Bacteria -0.0003903991  0.1339730
## 11 Total.dissolved.inorganic.nitrogen -0.0019997291  0.3029126
## 12      Soluble.reactive.phosphorus  0.0032110716  0.2765547
```

```
glimpse(final)
```

```
## Observations: 8292
## Variables:
## $ Day.number (dbl) 343.35, 346.70, 350.05, 353.40, 356.75, 360.10, 363...
## $ variable   (fctr) Ostracods, Ostracods, Ostracods, Ostracods, Ostrac...
## $ value      (dbl) 0.0000000000, 0.0000000000, 0.0000000000, 0.0000000...
## $ fr.value   (dbl) 0.0000000, 0.0000000, 0.0000000, 0.0000000, 0.00000...
## $ trend      (dbl) 0.03615422, 0.03640559, 0.03666087, 0.03690811, 0.0...
## $ dt.value   (dbl) -0.03615422, -0.03640559, -0.03666087, -0.03690811,...
## $ stand.y    (dbl) -0.1638576, -0.1650128, -0.1661861, -0.1673225, -0....
## $ y          (dbl) -0.03615422, -0.03640559, -0.03666087, -0.03690811,...
```

Zero removal

The time series of cyclopoid copepods, protozoa, filamentous diatoms, harpacticoid copepods and ostracods contained long sequences of zero values. This does not imply that these species were absent from the food web during these periods, but that their concentrations were below the detection limit. Time series dominated by many zeros can bias the statistical analysis. Therefore, these time series were shortened to remove long sequences of zero values, before the data transformation. The transformed data of all species in the food web are shown in Figure S2.

This is not done. May need to be done only for analyses for Table 1.

Figure S1 (visualising the transformation)

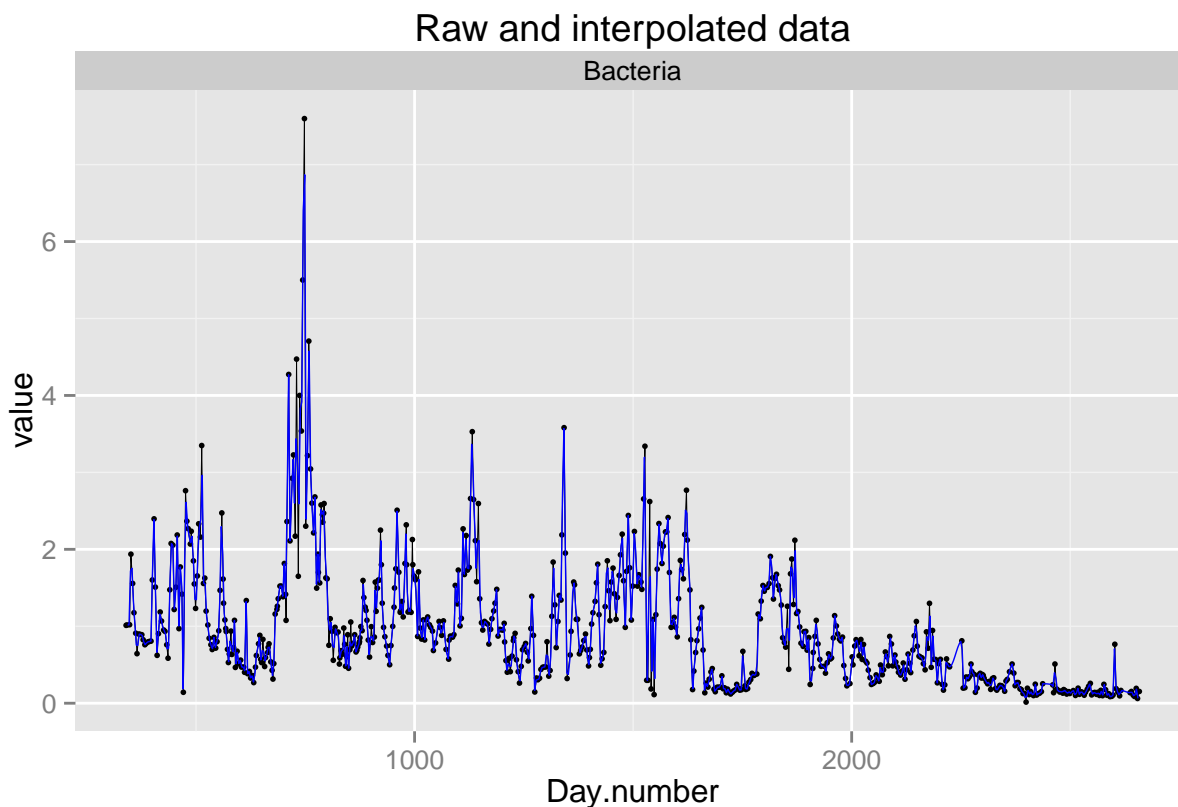
Choose a species to plot:

```
soi <- "Bacteria"
```

Raw and interpolated data:

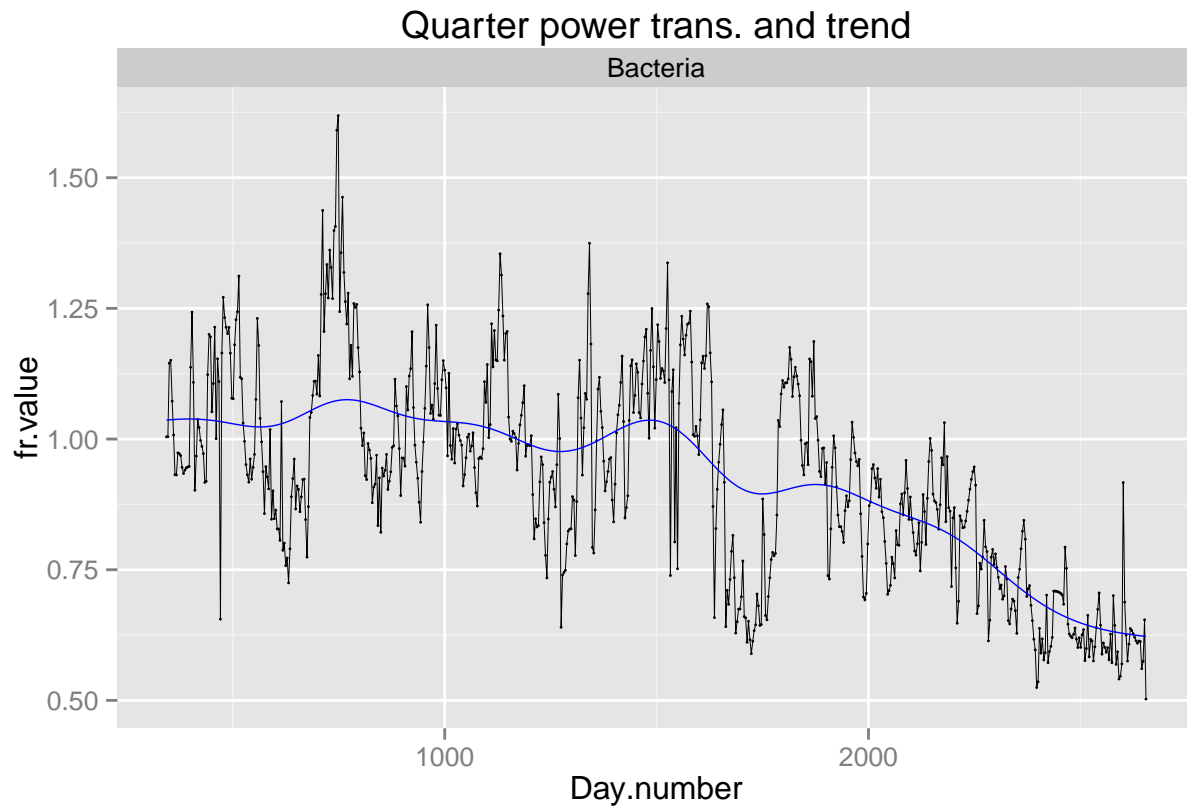
```
g1 <- ggplot(filter(all.data, variable==soi), aes(x=Day.number, y=value)) +  
  facet_wrap(~variable, ncol=2, scales="free_y") +  
  geom_point(size=1, col="black") + geom_line(size=0.1) +  
  scale_colour_manual(values = species.colour.mapping) + ggtitle("Raw and interpolated data")  
g2 <- geom_line(data=filter(final, variable==soi), aes(x=Day.number, y=value), size=0.25, col="blue")  
g1 + g2
```

Warning: Removed 17 rows containing missing values (geom_point).



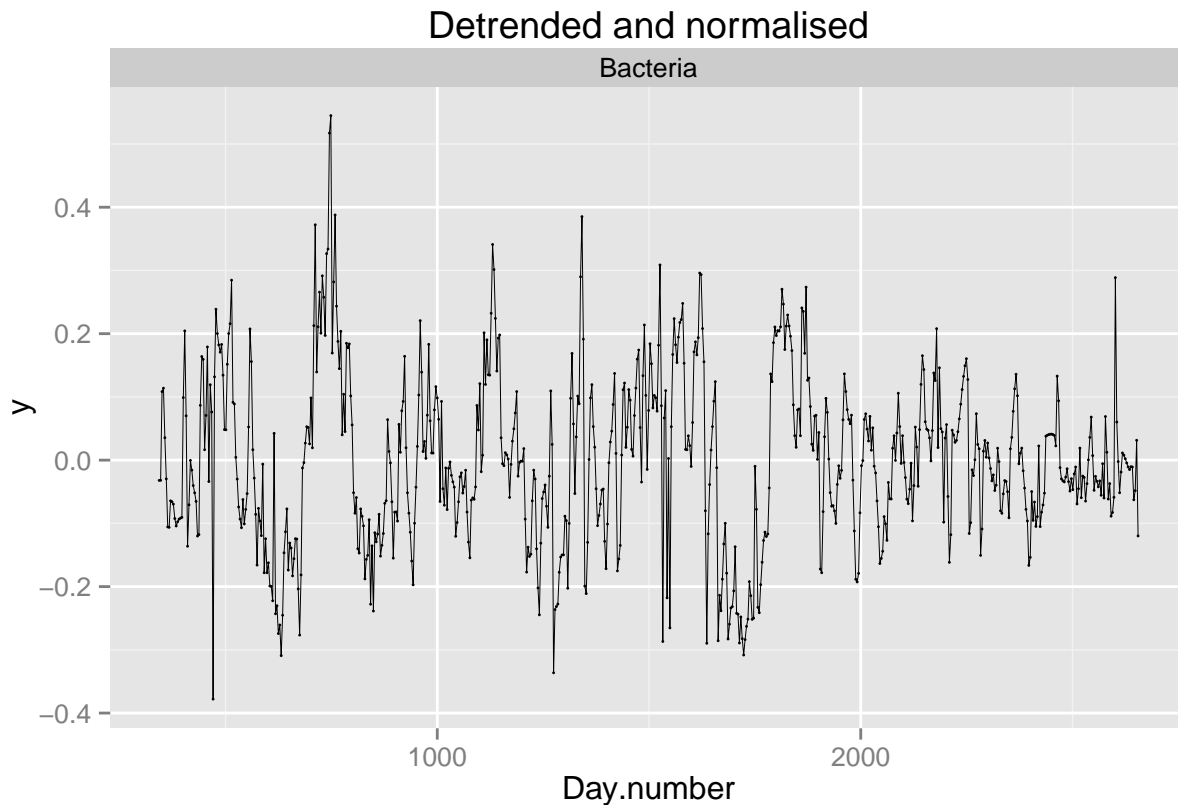
Fourth root transformed with trend:

```
g1 <- ggplot(filter(final, variable==soi), aes(x=Day.number, y=fr.value)) +  
  facet_wrap(~variable, ncol=2, scales="free_y") +  
  geom_point(size=0.5, col="black") + geom_line(size=0.1) +  
  scale_colour_manual(values = species.colour.mapping) + ggtitle("Quarter power trans. and trend")  
g2 <- geom_line(data=filter(final, variable==soi), aes(x=Day.number, y=trend), size=0.25, col="blue")  
g1 + g2
```



Detrended and normalised:

```
g1 <- ggplot(filter(final, variable=="soi"), aes(x=Day.number, y=y)) +
  facet_wrap(~variable, ncol=2, scales="free_y") +
  geom_point(size=0.5, col="black") + geom_line(size=0.1) +
  scale_colour_manual(values = species.colour.mapping) + ggtitle("Detrended and normalised")
g1
```



Compare the data made above to published data

Now take a look at the transformed data provided in the ELE Supplement, in the data sheet *transformed_data_Nature2008*.

First note that the data in the ELE supplement include a data point at day 2658.1, whereas the data above finish at 2654.85. This is because the real data end at 2658, and the interpolation method above doesn't want to create data outside the range of the original data.

The graph isn't produced here, as there is a mismatch in days abundances were interpolated to. Should fix this...

```
## Warning in `[<-.factor`(`*tmp*`, ri, value = structure(c(495L, 496L,
## 497L, : invalid factor level, NA generated
```

```
## Warning: Removed 324 rows containing missing values (geom_point).
```

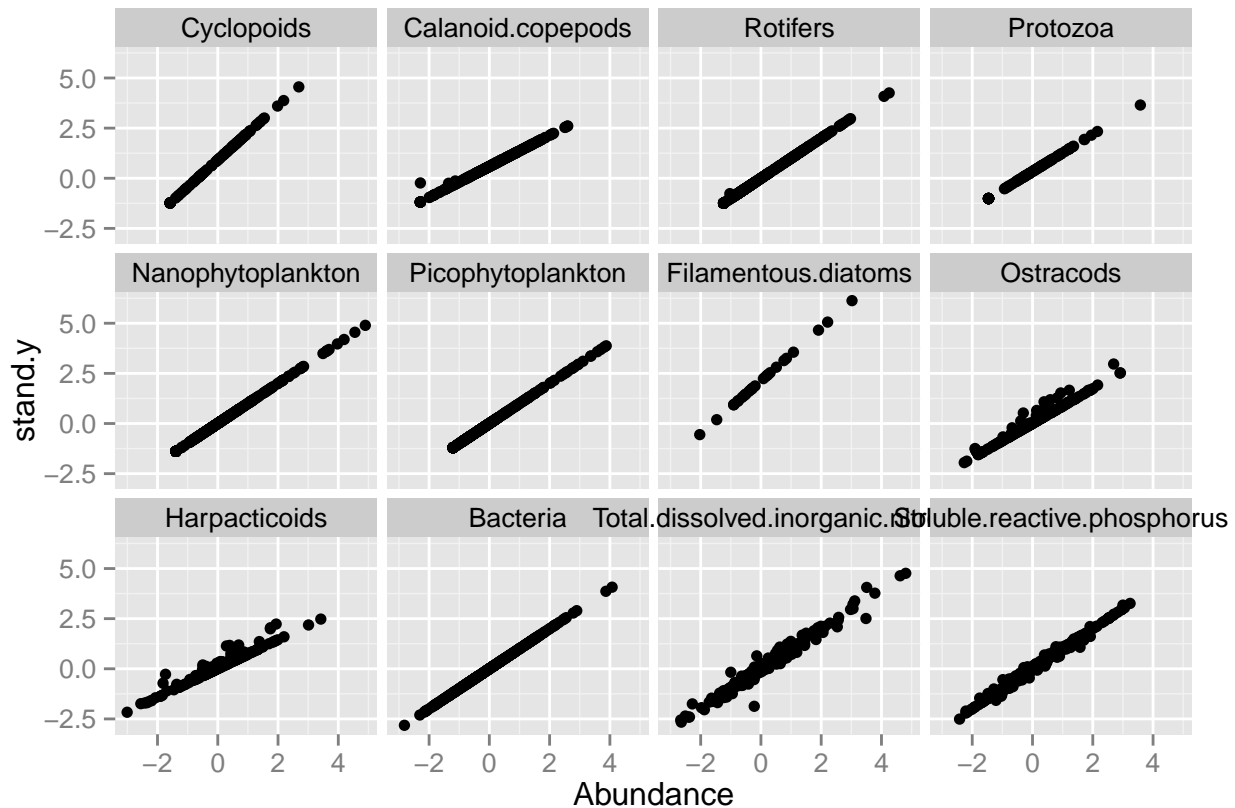
```
## Warning: Removed 130 rows containing missing values (geom_point).
```

```
## Warning: Removed 347 rows containing missing values (geom_point).
```

```
## Warning: Removed 413 rows containing missing values (geom_point).
```

```
## Warning: Removed 199 rows containing missing values (geom_point).
```

```
## Warning: Removed 239 rows containing missing values (geom_point).
```

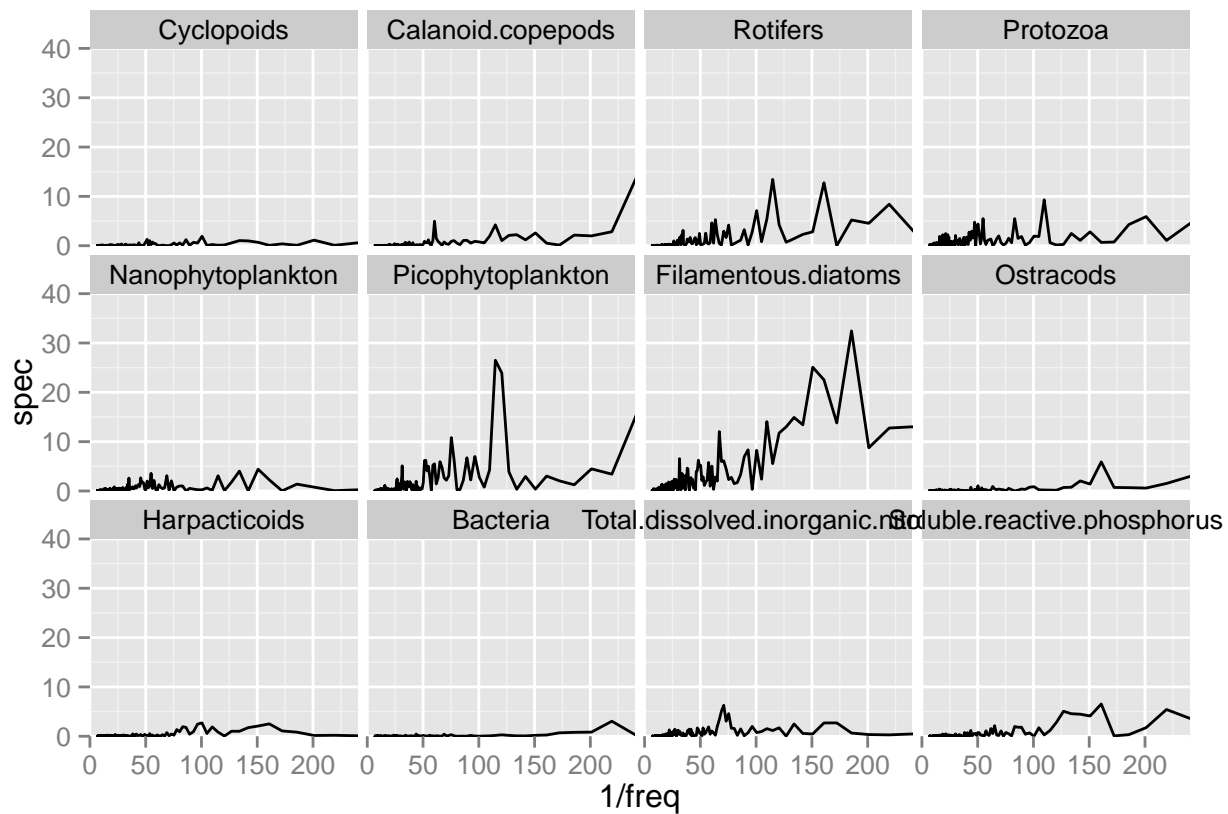


Looks OK, but suggests / shows that that data in the ELE supplement were standardised after removal of the zeros, whereas we don't do any zero removal (this is the same as in Ellner's code.)

Spectral analyses

```
# Raw spectrum
spectra <- final %>% group_by(variable) %>% do(spectra = spectrum(ts(data=.$y, end=2650.15, deltat=3.35),
spec <- spectra %>% do(data.frame(spec = .$spec[[2]], freq = .$spec[[1]], group = .[[1]]))

ggplot(spec, aes(y=spec, x=1/freq, group=group)) + geom_line() + facet_wrap(~group) +
coord_cartesian(ylim=c(0,40), xlim=c(0,240))
```



```
freq.est <- spec %>% group_by(group) %>% mutate(max_spec = max(spec), freq = freq)
```

```
## Warning: Grouping rowwise data frame strips rowwise nature
```

```
freq.est <- subset(freq.est, max_spec==spec, select=c(freq,group))
```

```
freq.est$freq <- 1/freq.est$freq
```

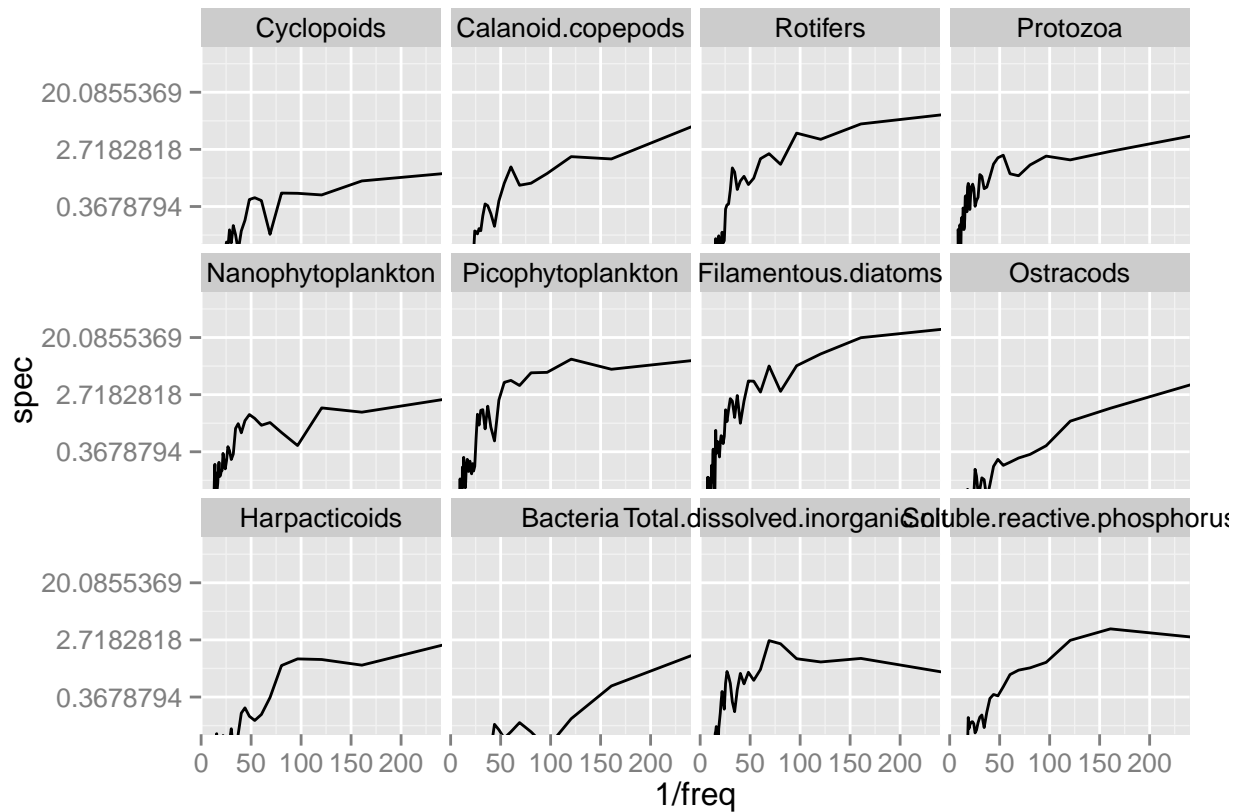
```
#freq.est
```

```
# Welch's periodogram
```

```
wspectra <- final %>% group_by(variable) %>% do(spectra = pwelch(ts(data=.$y, end=2650.15, deltat=3.35)
```

```
wspec <- wspectra %>% do(data.frame(spec = .$spec[[2]], freq = .$spec[[1]], group = .[[1]]))
```

```
ggplot(wspec, aes(y=spec, x=1/freq, group=group)) + geom_line() + facet_wrap(~group) +  
coord_cartesian(ylim=c(0.1,100), xlim=c(0,240))+  
scale_y_continuous(trans="log")
```



```
freq.est <- wspec %>% group_by(group) %>% mutate(max_spec = max(spec), freq = freq)
```

```
## Warning: Grouping rowwise data frame strips rowwise nature
```

```
freq.est <- subset(freq.est, max_spec==spec, select=c(freq,group))
freq.est$freq <- 1/freq.est$freq
#frequency(final$y)
ts <- as.ts(final$y, frequency = 0.3)
#time(ts)
```

Reproducing Table 1 using ELE supplement data.

Create dataset with zeros removed for this table (note that this is probably not how Beninca et al did this):

```
final_nozeros <- final
final_nozeros$y <- ifelse(final_nozeros$y!=0, final_nozeros$y, NA)
# make it wide format
#
final_long <- final_nozeros[final_nozeros$variable!="Cyclopoids" & final_nozeros$variable!="Filamentous"]
final_wide <- spread(as.data.frame(final_long), variable, stand.y)
# we also removed data on Cyclopoids, not used in the table
```

Calculate correlation coefficients:


```
cor.coefs <- cor(final_wide[,c(-1)])
```

Only keep the upper triangle of the cor.pvals matrix:

```
for(i in 1:10){  
  for(j in 1:10){  
    cor.coefs[i,j] <- ifelse(i<j, cor.coefs[i,j], NA)  
  }  
}
```

Get p-vals too:

```
# https://stat.ethz.ch/pipermail/r-help/2005-July/076050.html  
pn <- function(X){crossprod(!is.na(X))}  
cor.prob <- function(X){  
# Correlations Below Main Diagonal  
# Significance Tests with Pairwise Deletion  
# Above Main Diagonal  
# Believe part of this came from Bill Venables  
pair.SampSize <- pn(X)  
above1 <- row(pair.SampSize) < col(pair.SampSize)  
pair.df <- pair.SampSize[above1] - 2  
R <- cor(X, use="pair")  
above2 <- row(R) < col(R)  
r2 <- R[above2]^2  
Fstat <- (r2 * pair.df)/(1 - r2)  
R[above2] <- 1 - pf(Fstat, 1, pair.df)  
R  
}  
cor.pvals <- cor.prob(final_wide[,c(-1)])
```

Only keep the upper triangle of the cor.pvals matrix:

```
for(i in 1:10){  
  for(j in 1:10){  
    cor.pvals[i,j] <- ifelse(i<j, cor.pvals[i,j], NA)  
  }  
}
```

Add significance “stars” to cor.coefs from cor.pvals

```
cor.stars <- cor.pvals  
cor.stars <- ifelse(cor.pvals<0.0001, "***",  
                   ifelse(cor.pvals<0.001, "**",  
                           ifelse(cor.pvals<0.05, "*", "")))
```

```
cor.cp <- cor.coefs  
for(i in 1:10){  
  for(j in 1:10){  
    cor.cp[i,j] <- paste(round(cor.coefs[i,j],3), cor.stars[i,j])  
  }  
}
```

Remove NAs:

```

for(i in 1:10){
  for(j in 1:10){
    cor.cp[i,j] <- ifelse(cor.cp[i,j]=="NA NA", "", cor.cp[i,j])
  }
}
for(i in 1:10){
  for(j in 1:10){
    cor.cp[i,j] <- ifelse(i==j, "1", cor.cp[i,j])
  }
}

colnames(cor.cp) <- c("Calanoid.copepods ", "Rotifers ", "Protozoa ", "Nanophytoplankton ", "Picophytoplankton ",
"Ostracods ", "Harpacticoid.copepods ", "Bacteria ", "Nitrogen ", "Phosphorus ")
rownames(cor.cp) <- colnames(cor.cp)

```

Make it a table:

```

library(knitr)
table1b <- kable(cor.cp, format="html", col.names = colnames(cor.cp), align="c",
                 caption="Table 1.'Correlations between the species in the food web. Table entries show the product-moment correlation coefficients, after transformation of the data to stationary time series (see Methods). Significance tests were corrected for multiple hypothesis testing by calculation of adjusted P values using the false discovery rate.' Significant correlations are indicated as follows: :  $P<0.05$ ; :  $P<0.01$ ; :  $P<0.001$ . 'The correlation between calanoid copepods and protozoa could not be calculated, because their time series did not overlap. Filamentous diatoms and cyclopoid copepods were not included in the correlation analysis, because their time series contained too many zeros.' (Beninca et al. 2008)
")
table1b

```

Table 1.'Correlations between the species in the food web. Table entries show the product-moment correlation coefficients, after transformation of the data to stationary time series (see Methods). Significance tests were corrected for multiple hypothesis testing by calculation of adjusted P values using the false discovery rate.' Significant correlations are indicated as follows: : $P<0.05$; : $P<0.01$; : $P<0.001$. 'The correlation between calanoid copepods and protozoa could not be calculated, because their time series did not overlap. Filamentous diatoms and cyclopoid copepods were not included in the correlation analysis, because their time series contained too many zeros.' (Beninca et al. 2008)

Calanoid.copepods

Rotifers

Protozoa

Nanophytoplankton

Picophytoplankton

Ostracods

Harpacticoid.copepods

Bacteria

Nitrogen

Phosphorus

Calanoid.copepods

1

-0.032

-0.281 ***

0.106 *

-0.101 *

-0.032

-0.122 *

0.079 *

0.024

-0.025

Rotifers

1

-0.004

-0.191 ***

-0.029

0.234 ***

0.15 ***

0.296 ***

-0.041

0.099 *

Protozoa

1

0.137 **

-0.034

0.116 *

0.001

-0.131 **

0.034

0.088 *

Nanophytoplankton

1

-0.174 ***

-0.097 *

-0.03

-0.168 ***

-0.021

0.03

Picophytoplankton

1

-0.045

-0.039

0.031

```

-0.001
-0.04
Ostracods
1
0.414 ***
0.078 *
-0.098 *
0.137 **
Harpacticoid.copepods
1
0.084 *
-0.063
0.106 *
Bacteria
1
0.052
0.181 ***
Nitrogen
1
0.084 *
Phosphorus
1

```

```
# differs from the one published by Beninca et al.!
```

```
->
```

Predictability (Figure 2)

This will be done after getting global Lyapunov exponents by the indirect method.

Lyapunov exponents by direct method (Figure 3)

Estimate the Lyapunov exponents of the time series, via time-delayed embedding. The Nature report used the [Tisean software](#), which was available from CRAN [until mid 2014](#). Based on this, and being a bit less well integrated with R, we'll instead use the [tseriesChaos](#) package, which was *largely inspired by the TISEAN project*.

Unclear if this was performed on untransformed or transformed data. First try with the transformed data. Time delay (1), embedding dimension (6), and Theiler window (50) were used in the Nature report. Other parameters are chosen rather randomly, though don't seem to matter too much.

```
time.delay <- 1
embedding.dimension <- 6
Theiler.window <- 50
```

Note that a time step is 3.35 days in the transformed data. So to get a graph with 80 days on the x-axis (as in Figure 3 in the Nature report), we need $80/3.35 = 24$ time steps for the calculation of Lyapunov exponents.

```
time.steps <- 24
```

Remove the species that were not analysed in the Nature report, due to too many zeros in the time series:

```
led <- filter(tr, variable!="Filamentous.diatoms",
             variable!="Protozoa",
             variable!="Cyclopoids")
```

Get the data for the graphs:

```
all.species <- unique(as.character(led$variable))
diverg <- matrix(NA, time.steps, length(all.species))
colnames(diverg) <- all.species
for(i in 1:length(all.species)) {
  print(all.species[i])
  tr.fs <- filter(final, variable==all.species[i])$y
  diverg[,i] <- as.numeric(try(lyap_k(tr.fs,
                                     m=embedding.dimension,
                                     d=time.delay,
                                     k=10, # number of considered neighbours 20
                                     ref=40, # number of points to take into account 100
                                     t=Theiler.window,
                                     s=time.steps,
                                     eps=10 # radius where to find nearest neighbours 10
                                     )))
}
```

```
## [1] "Calanoid.copepods"
## Finding nearests
## Keeping 40 reference points
## Following points
## [1] "Rotifers"
## Finding nearests
## Keeping 40 reference points
## Following points
## [1] "Nanophytoplankton"
## Finding nearests
## Keeping 40 reference points
## Following points
## [1] "Picophytoplankton"
## Finding nearests
## Keeping 40 reference points
## Following points
## [1] "Ostracods"
## Finding nearests
```

```

## Keeping 40 reference points
## Following points
## [1] "Harpacticoids"
## Finding nearests
## Keeping 40 reference points
## Following points
## [1] "Bacteria"
## Finding nearests
## Keeping 40 reference points
## Following points
## [1] "Total.dissolved.inorganic.nitrogen"
## Finding nearests
## Keeping 40 reference points
## Following points
## [1] "Soluble.reactive.phosphorus"
## Finding nearests
## Keeping 40 reference points
## Following points

## a bit of a fudge with the translation to days
diverg <- as.data.frame(cbind(days=1:time.steps, diverg))
diverg <- gather(diverg, Species, Difference, 2:10)
diverg$days <- diverg$days*3.35
#str(diverg)

```

Next calculate the Lyapunov exponents, noting that 6 or 7 points were used in the regressions in the Nature report

```

diverg$Difference[is.na(diverg$Difference)] <- 0
diverg$Difference[is.infinite(diverg$Difference)] <- 0
diverg.short <- filter(diverg, days<24) ## 24 is about 6 steps, after initial gap
LEs <- group_by(diverg.short, Species) %>%
  summarise(le=coef(lm(Difference[1:6] ~ days[1:6]))[2])
#pval=summary(lm(Difference[1:6] ~ days[1:6]))$coefficients[2,4])

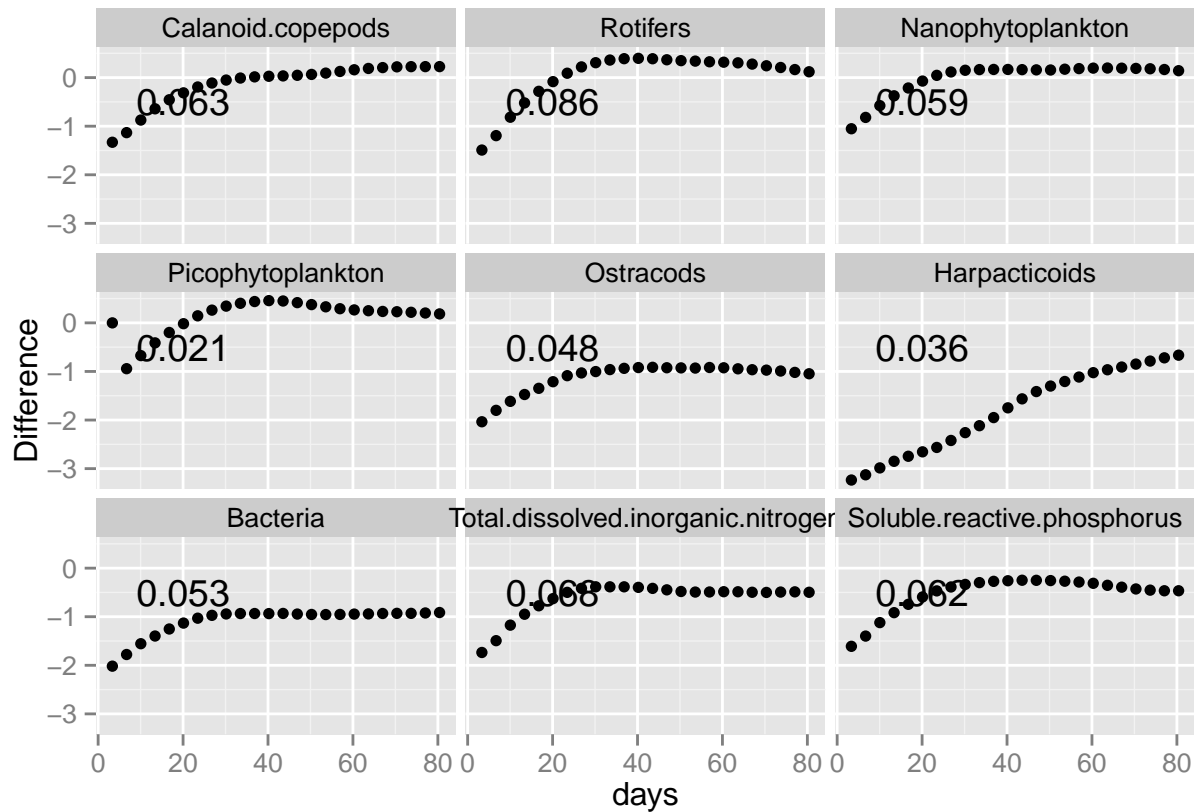
```

Then plot the graphs with LE:

```

LEs <- mutate(LEs, days=20, Difference=-0.5)
g1 <- ggplot(diverg, aes(x=days, y=Difference)) + geom_point() + facet_wrap(~Species) +
  geom_text(data=LEs, aes(label=round(le,3)), group=NULL)
g1

```



Not exactly the same as Figure 3 in the Nature report. Qualitatively the same, except for where the time-delayed embedding failed.

Lyapunov exponents by indirect method

The functions used in the code below are based on code received from Stephen Ellner. The modifications have been tested, and produce the same results as Ellner's original code.

The function needs a matrix, X, with species abundances in wide format. Be careful to work on the unstandardised data (or standardised, if you wish) (comment out appropriate lines here).

```
## use next line to work on unstandardised data
final.to.melt <- final[, c("variable", "dt.value", "Day.number")]
## use next line to work on standardised
#final.to.melt <- final[, c("variable", "y", "Day.number")]

names(final.to.melt)[1] <- "Species"
melted <- melt(final.to.melt, id=c("Species", "Day.number"))
X <- acast(melted, formula= Day.number ~ Species)
#str(X)
X <- as.data.frame(X)
```

Restrict range of data appropriately:

```
## Select the time period to use
start.longest=334; start.longer=808; start.shorter=1035;
```

```
e=as.numeric(row.names(X)) > start.longer; X=X[e,];
e=as.numeric(row.names(X)) < 2654; X=X[e,];
```

Load and run the functions, or read in from data file (default option, for which you will need to change the path to the data file.)

```
# read script lines from website
script <- getURL("https://raw.githubusercontent.com/opetchey/RREEBES/Beninca_development/Beninca_etal_2008_Nature/data/gle_estimates.R")

# parse lines and evaluate in the global environment
eval(parse(text = script))

## don't run this as it takes a while
#LE <- Get_GLE_Beninca(X)
#save(LE, file=~ /Desktop/GLE_estimate.Rdata")

## load the already saved data from github (this can take some time depending on the internet connection)
source_data("https://github.com/opetchey/RREEBES/raw/Beninca_development/Beninca_etal_2008_Nature/data/gle_estimates.R")

## Downloading data from: https://github.com/opetchey/RREEBES/raw/Beninca_development/Beninca_etal_2008_Nature/data/gle_estimates.R
##
## SHA-1 hash of the downloaded data file is:
## f77a72a8058f8e3a5ec7752abeeaa78e3fffa368

## [1] "LE"
```

```
LE[[1]]
```

```
## [1] 0.03748704
```

This is quite far from the number using code and data from Steve (0.08415112). But recall that the functions have been carefully checked. Probably it is the data going into this function. A final step would be to save the data here, and take it into Steve's function. (This point is an issue on github.)

Predictability (Figure 2)

Need to predict until about 40 days ahead = $40 / 3.35$ time steps = 12 time steps.

Do this from each time in the time series as initial abundances.

From each time in the series, predict 12 steps ahead. Put results in an array: time x species, start.location time will be 12 species will be 12 start location will be length of time series - 12

```
x <- X

Z <- LE[[3]]
Z1 <- Z[,13:24]

all.species <- names(all.gams)

time.to.predict <- 12
```



```

nn <- length(Z1[,1])-time.to.predict

preds <- array(NA, c(12, 12, nn))

dimnames(preds) <- list(dist=1:12,
                        species=all.species,
                        start.time=1:nn)
for(i in 1:length(all.species))
  preds[1,i,] <- predict(all.gams[[i]])[1:nn]

#for(i in 1:length(all.species))
#  print(length( predict(all.gams[[i]])))

```

Look at the correlation between observed and predicted abundances:

```

# layout(matrix(1:12, 4, 3))
# for(soi in all.species){
#   xxx <- Z1[1:nn,soi]
#   yyy <- preds[1, soi, ]
#   plot(xxx, yyy,
#        xlab="Observed abundance",
#        ylab="Predicted abundance",
#        main=paste(soi, "rsq =", round(cor(xxx,yyy)^2,2)))
# }

```

Now for the predictions at t+2 from predictions at t+1

```

pred.time <- 2
for(pred.time in 2:12) {
  for(i in 1:length(all.species))
    preds[pred.time,i,pred.time:nn] <- predict(all.gams[[i]],
                                                newdata=as.data.frame(t(preds[pred.time-1,,]))[pred.time,])
}

```

Get the correlations and do some house keeping:

```

cors <- matrix(NA, 12, 12)
dimnames(cors) = list(dist=1:12,
                      species=names(x))
for(i in 1:12) {
  for(j in 1:12) {
    cors[j,i] <- cor(Z1[1:nn,i], preds[j, i, ], use="complete.obs")^2
  }}

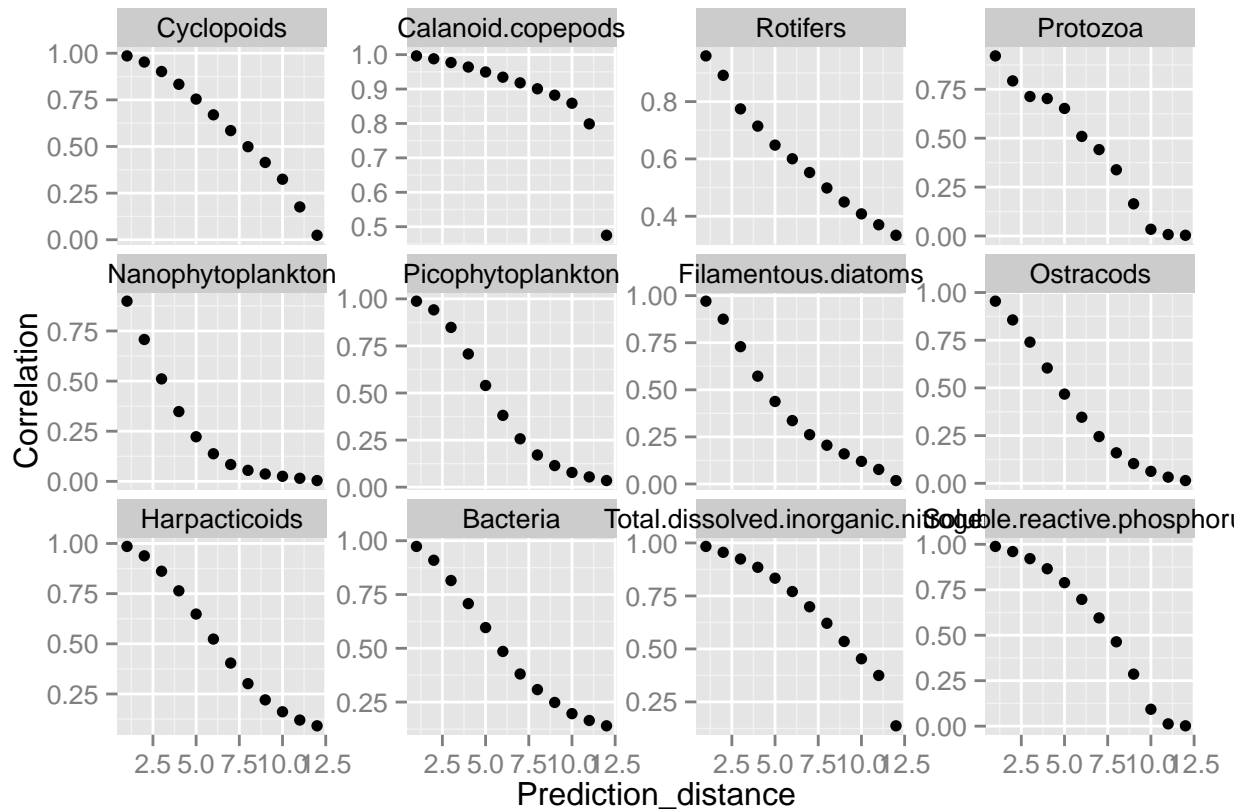
cors <- data.frame(dist=as.numeric(I(rownames(cors)))), cors)
cors.long <- gather(as.data.frame(cors), key=dist)

names(cors.long) <- c("Prediction_distance", "Variable", "Correlation")

```

And plot our version of figure 2:

```
ggplot(cors.long, aes(x=Prediction_distance, y=Correlation)) +
  geom_point() +
  facet_wrap(~Variable, scales="free_y" )
```



First pass working. Need to double check everything. Quite different patterns from in figure 2 of the nature paper. There is relatively little information in the paper or supplement about how figure 2 data was produced, so difficult to pin down the difference without asking authors.