

# 9. Temporal Diversity

Z620: Quantitative Biodiversity, Indiana University

## OVERVIEW

Biological diversity varies through time in response to changes in the biotic and abiotic environment. Rising temperatures and CO<sub>2</sub>, trends in precipitation and drought, and the dynamics of migration and colonization of species are just a few factors that influence biodiversity through time. While some biologists focus on processes that occur on contemporary scales (minutes, days, weeks, years), other scientists are interested in the forces that drive patterns of biodiversity in the fossil record and over geologic time scales. In this handout, we will strengthen our “data wrangling” skills and add a temporal dimension to the site-by-species matrix. You will then learn the basics of time series analysis, repeated-measures analysis of variance, temporal beta diversity (e.g., turnover), while touching on topics related to community stability.

## 1) SETUP

### Retrieve and Set Your Working Directory

```
rm(list=ls())
getwd()
setwd("~/GitHub/QB-2025/1.HandOuts/9.TemporalDiversity")

# Recall, in Posit.cloud, set your working directory as follows:
#setwd("/cloud/project")
```

### Install Packages

This module will require several R packages. We will describe the packages in greater details in the sections below. For now, let's just load them. The `require()` function in R returns `TRUE` if the package was successfully loaded or `FALSE` if the package failed to load. This `for` loop loads each package and installs the package when `require()` returns `FALSE`.

```
package.list <- c('vegan', 'tidyr', 'dplyr', 'codyn', 'ggplot2',
  'cowplot', 'MullerPlot', 'RColorBrewer', 'reshape2', 'lubridate',
  'TTR', 'xtable', 'multcomp', 'pander', 'png', 'grid', 'tseries', 'nlme',
  'forecast', 'emmeans')
for (package in package.list) {
  if (!require(package, character.only = TRUE, quietly = TRUE)) {
    install.packages(package, repos='http://cran.us.r-project.org')
    library(package, character.only = TRUE)
  }
}
```

## 2) LOADING DATA

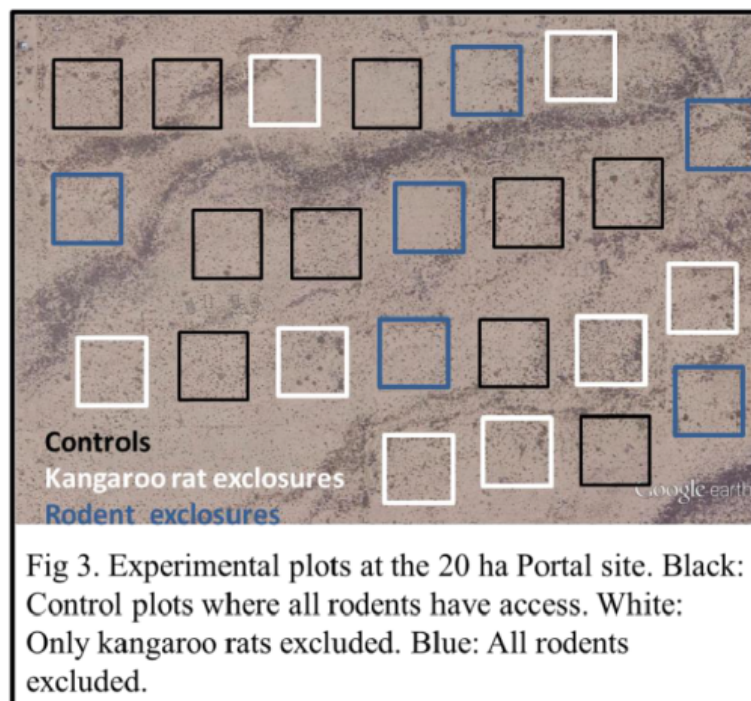
To learn about topics of temporal diversity, we will use the long-term rodent dataset from the Chihuahuan Desert ecosystem near Portal, Arizona. Known as the “Portal Project” (<http://portal.weecology.org/>), this research site was initiated in 1977 by Jim Brown and colleagues to study species interactions, specifically competitive dynamics within and among species of rodents and ants. Once every month since its inception, members of the Portal Project monitor 24 experimental plots, each 0.25 ha in area (50 X 50 m). In total, 4.8 kilometers of fencing is used to maintain the Portal experiment!

Let’s take a look at the data:

```
portal <- read.table("data/combined.csv", sep = ",", header = TRUE)
```

Take a few minutes to explore the structure of this dataset. The version of the data that we are working with spans from 1977 - 2002. During this period, individual rodents were captured from plots (“plot\_id”), identified to species (“species\_id”), which led to the creation of a “record\_id” with an associated date (day, month, and year). In addition, the sex, size (“hindfoot\_length” and “weight”) and taxonomic identity (“genus” and “species”) of animals were recorded. All of this was done in five experimentally replicated treatments (see Figure below):

- 1) Controls - fencing around plots does not exclude rodents (plot\_id: 2, 4, 8, 11, 12, 14, 17, 22)
- 2) Long-term Krat - long-term exclusion of Kangaroo rats (*Dipodomys* spp.) (plot\_id: 3, 15, 19, 21)
- 3) Short-term Krat - short-term exclusion of Kangaroo rats (*Dipodomys* spp.) (plot\_id: 6, 13, 18, 20)
- 4) Rodent Exclosure - exclusion of all rodents (plot\_id: 5, 7, 10, 16, 23, 24)
- 5) Spectab exclosure - exclusion of Banner-tailed kangaroo rat (*Dipodomys spectabilis*) (plot\_id: 1, 9)



### 3) DATA WRANGLING

One thing you may notice when looking at `portal` is that it has a lot of observations, almost 35,000 (and remember this is only 1977 - 2002). These data are entered in **long format**, which means that each row represents a unique observation (i.e., a trapped animal). The long format is a convenient way to enter data that reduces the probability of entry errors. However, manipulating long-format data for visualization and statistical analysis requires some manipulation. For example, many R packages and functions require you to organize your data in **wide format** where different sampling time points would be represented in columns.

In the following sections, we will demonstrate how to manipulate the `portal` data set to carry out different types of analyses using functions from the `dplyr` and `tidyr` packages. These packages were especially designed for transforming, subsetting, and summarizing tabular data (i.e., data within tables). The functions contained in these two packages – as well as other functions in the R base package like `apply()` and `aggregate()` – are preferred for manipulating data in R because they are faster and more efficient than other control-flow statements (e.g., loops) that are commonly used in other programming languages.

First, let's use the `unite()` function from the `tidyr` package to create new columns that contain information in other columns. The “remove = FALSE” statement retains the original data vectors.

```
# Make a date vector that contains year, month, and day
portal <- unite(portal, col = date, c(year, month, day), sep = "-", remove = FALSE)

# Make a taxon vector that contains genus and species names
portal <- unite(portal, col = taxon, c(genus, species), sep = "_", remove = FALSE)
```

Now, we are going to use `dplyr` to create a **time-by-species matrix**. To do this, we are going to use a new operator referred to as a “pipe” (`%>%`). Pipes allow output from one function to be used as input for another function, all in the same line of code. When using pipes, the output from the function to the left becomes the input for the function on the right.

In the following R chunk, we will build a time-by-species matrix. First, we will use a `dplyr` function called `group_by()`, which splits the dataset up according the variable(s) supplied. We then use the `count()` function to sum the number of individuals belonging to each taxon while maintaining the year and `plot_id` grouping. The `fill` argument assigns a value of zero if there are no values for a given combination of groupings. Finally, we use the `spread()` function from `tidyr` to convert the long format output of the `count()` function into a wide format dataset. The `key =` argument specifies the new column names and the `value =` argument specifies the values that will become the elements of the wide form dataset.

```
time.by.species <- group_by(portal, year, plot_id) %>%
  count(taxon) %>% spread(key = taxon, value = n, fill = 0)
```

Take a moment to inspect the structure of the `time.by.species` object we just created. From this data structure, we can retrieve different different types of information. For example, if we want the site-by-species matrix for 1984 we can use the following code:

```
dplyr::filter(time.by.species, year == 1984)
```

And if we want the species data from plot 5 for all years, we use the following code:

```
dplyr::filter(time.by.species, plot_id == 5)
```

Last, let's convert the `tidyr` object to a data frame so it can be used with functions from other packages:

```
time.by.species <- as.data.frame(time.by.species)
```

## 4) TIME SERIES ANALYSIS - A PRIMER

In this section, we introduce some basic concepts and tools used in time series analysis. One goal of time series analysis is to detect and decompose trends in temporal data. Ideally, these trends should be independent from other sources of variability (e.g., seasonality, cycles, and sampling error). Another goal of time series analysis is to make **forecasts** about a system, that is, predictions of future behavior. We will demonstrate some of these tools using the abundance of rodents for a single site in the Portal Project. Throughout the year, total rodent abundance may fluctuate widely in response to environmental change, e.g., precipitation. Because the Chihuahuan Desert sits in a rain shadow created by the Sierra Madre Mountains, the Portal site is an arid ecosystem with rain falling mostly during the months of June through October. This variability in precipitation provides an opportunity for us to detect a signal of this **seasonality** using time series analysis while also testing for long-term trends and forecasting rodent densities into the future.

### Data wrangling

In the following R chunk, we manipulate `portal` using some of the tools introduced above from the `dplyr` and `tidyr` packages. We use `count()` to sum the number of individuals belonging to each rodent taxon while maintaining the grouping by year, month, and `plot_id`. We retain month in this case so we can create a categorical variable called “season”.

```
# Create a time-by-species matrix that includes year, month, and plot_id
time.by.spec.2 <- filter(portal, taxa=="Rodent") %>%
  group_by(year, month, plot_id) %>%
  count(taxon)

# Create a seasonality variable using month number (6 = June; 10 = October)
time.by.spec.2$season <- NA
time.by.spec.2$season <- time.by.spec.2$month %in% c(6:10)

# Rainy seasons are June - October
time.by.spec.2$season <- ifelse(time.by.spec.2$season == TRUE, "rain", "norain")

# Group the data by year and season
group_by(time.by.spec.2, year, season)
```

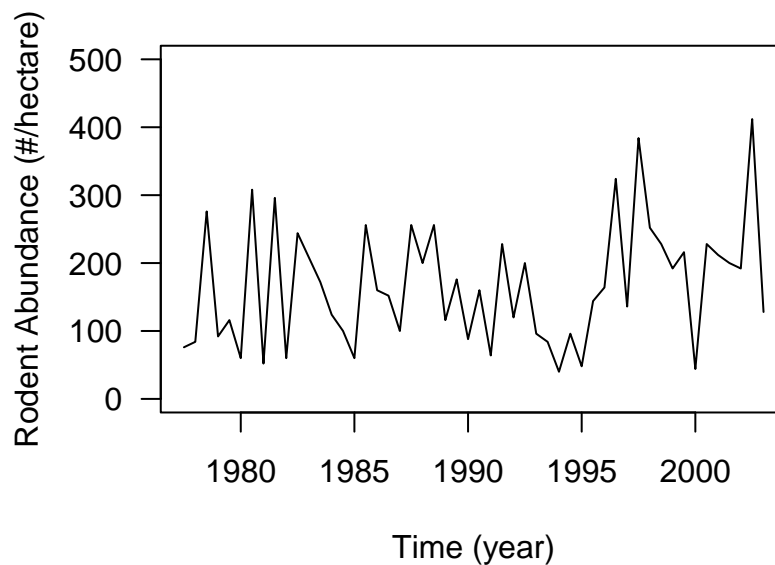
Now we are going to use the `filter()` function in `dplyr` to pick a plot. Next, we calculate rodent abundance per hectare ( $0.25 \text{ ha} * 4 = 1 \text{ ha}$ ) for each season within a year. Then, we created a time series object (`.ts`) that identifies the start time and seasonality of our sampling, which is determined by the frequency argument. Time series objects (`.ts`) are vectors or matrices which represent data that has been sampled at equispaced points in time.

```
abund <- filter(time.by.spec.2, plot_id == 2) %>%
  group_by(year, season) %>%
  count(wt = n)

abund$n <- abund$n * 4

abund.ts <- ts(abund$n, frequency = 2, start = c(1977, 2))
```

```
plot.ts(abund.ts, type = "l", ylab = "Rodent Abundance (#/hectare)",
        xlab = "Time (year)", las = 1, ylim = c(0, 500))
```



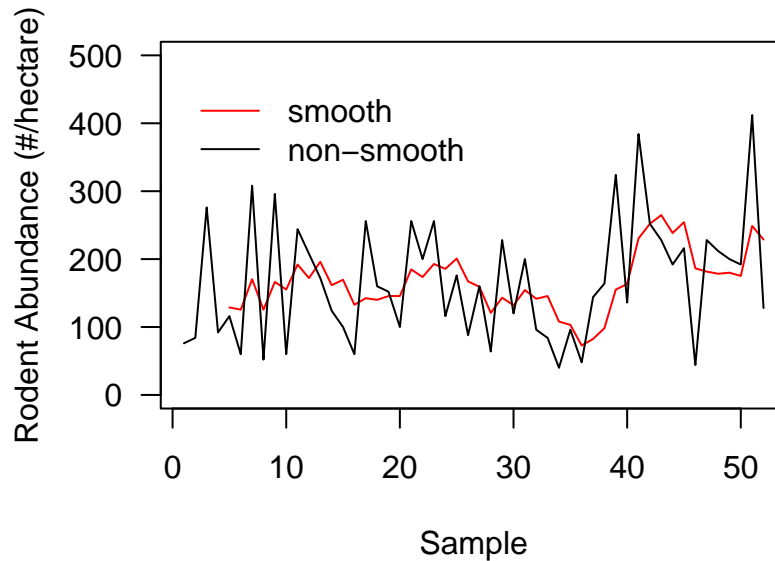
## Smoothing

One technique that is commonly used, mostly for visualizing trends in a time series is smoothing. Smoothing techniques attempt to remove noise, and are used to help detect signal in a dataset. The simplest form of smoothing is the **simple moving average**. Simple moving average calculates an unweighted arithmetic mean of your observations across a window of the past  $n$  observations.

In the following R chunk, we use the `SMA()` function contained in the `TTR` package. (Note that this package does not accept a `ts` object.) Change the value of  $n$  to visualize the effect of the smoothing window.

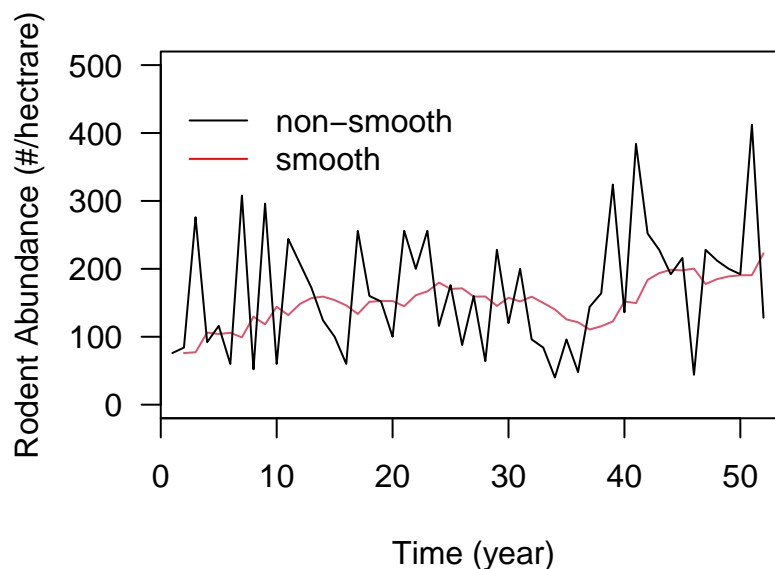
```
abund.sm <- SMA(abund$n, n = 5)

plot(abund.sm, type = "l", col = "red", ylab = "Rodent Abundance (#/hectare)",
     xlab = "Sample", las = 1, ylim = c(0, 500))
lines(abund$n, col = "black")
legend(0, 475, col = c("red", "black"), lty = c(1,1),
      c("smooth", "non-smooth"), bty = "n", cex = 1)
```



**Exponential smoothing** is another way to smooth a time series. This process places exponentially less weight on past observations. The Holt-Winters filtering technique is commonly used for exponential smoothing. In R, the `HoltWinters()` function in the `stats` package allows one to specify two parameters. The `beta` argument when set to `FALSE` performs exponential smoothing, while the `gamma` argument is used to specify seasonality. In the output, you will get an `alpha` parameter, which ranges from 0 to 1. Values closer to 1 indicate that the smoothing is influenced by current observations, while values closer to 0 indicate that more weight is placed on past observations.

```
abund.hw <- HoltWinters(abund$n, beta = FALSE, gamma = FALSE)
# abund.hw$fitted
plot(abund.hw, xlab = "Time (year)", ylim = c(0, 500),
     ylab = "Rodent Abundance (#/hectare)", las = 1, main = NA)
legend(0, 475, col = c("black", "red"), lty = c(1,1),
      c("non-smooth", "smooth"), bty = "n", cex = 1)
```



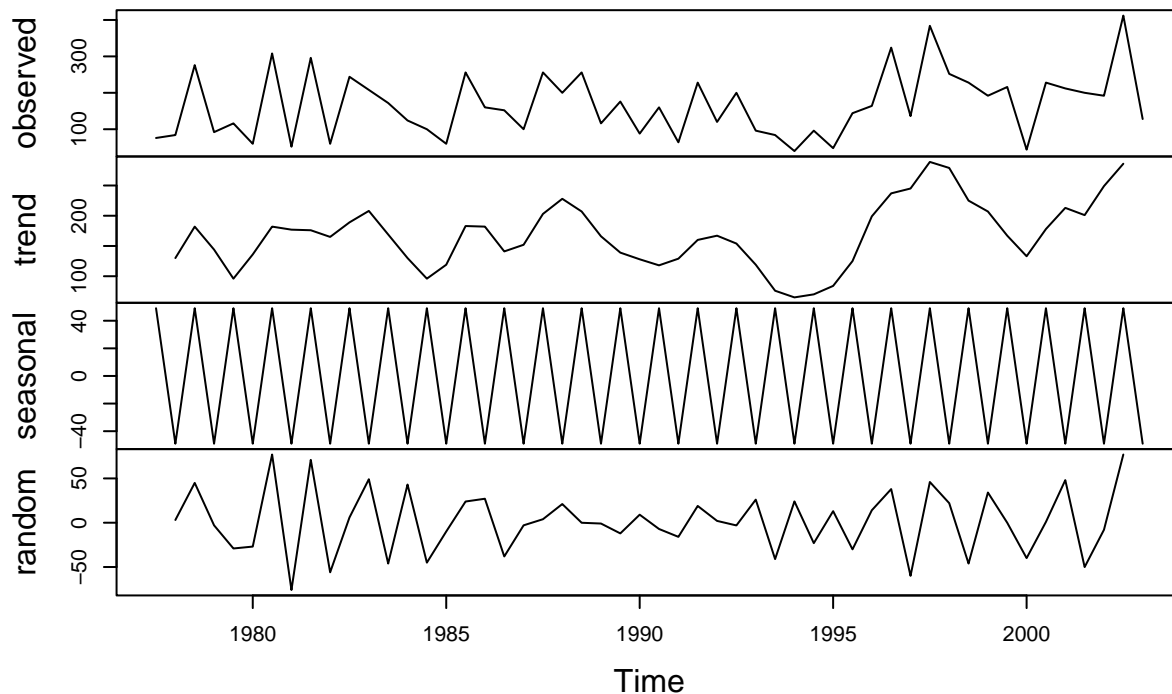
## Decomposition of a time series

A time series can be broken down into different “categories”, which can provide insight into factors contributing to temporal patterns. The common categories of a time series decomposition are the trend (i.e., increasing or decreasing value in the series), seasonality (repeating short-term cycles), and residual error (i.e., statistical noise due to stochastic changes or sampling error). As mentioned above, we subsampled the `portal` data set so that it included seasonal variation in precipitation. In the following R chunk, we will use the `decompose()` function to look at different decomposition categories. If seasonal trends are a nuisance in your study, there are ways to remove them, as done in the code below.

```
# moving average decomposition
abund.comp <- decompose(abund.ts)

# plot decomposition categories
plot(abund.comp)
```

## Decomposition of additive time series



```
# remove seasonality
abund.adj <- abund.ts - abund.comp$seasonal
```

## Autoregressive moving average (ARMA) models

Autoregressive is a stochastic process used in statistical analysis, in which future values are estimated based on a weighted sum of past values. An autoregressive process operates under the premise that past values have an effect on current values.

Autoregressive moving average (ARMA) models are commonly used to model time series. ARMA approaches can identify trends in data and help to make forecasts about future observations. As such, ARMA is often

used in biology and the environmental sciences, but also in business and economics. In this section we will walk through the basic steps of implementing ARMA in R.

The autoregressive component of an ARMA model uses regression to obtain *coefficients* that predict current observations using previous or “lagged” observations from a time series, which can be described with the following equation:

$$Y_t = c + \sum_{i=1}^p \phi_i Y_{t-i} + \epsilon_t$$

where  $Y_t$  is an observation at time  $t$ ,  $c$  is a constant,  $\epsilon$  is the error term, and  $\phi$  is the fitted parameter associated with the autoregressive order (or lag)  $p$ .

In this way, the data is regressed on previous data points, hence, “autoregressive” The moving average component of an ARMA model should not be confused with the moving average techniques that were described in the section above on smoothing. Rather, the moving average component of an ARMA model uses multiple regression to recover *error terms* of the current and prior observations, which can be described with the following equation:

$$Y_t = \mu + \epsilon_t + \sum_{i=1}^q \theta_i \epsilon_{t-i}$$

where  $\mu$  is the mean of the time series ( $Y$ ),  $\theta$  is fitted parameter, and  $\epsilon$  refers to errors associated with order (or lag)  $q$ . The full ARMA model can then be expressed as follows

$$Y_t = c + \sum_{i=1}^p \phi_i Y_{t-i} + \epsilon_t + \mu + \epsilon_t + \sum_{i=1}^q \theta_i \epsilon_{t-i}$$

**Assumptions of stationarity** If the mean, variance, or covariance in a time series is affected by time, then we are likely to be violating the assumption of **stationarity**. If the assumption of stationarity is not met, corrective measures should be taken, which could involve transforming or differencing the data. In the following R chunk, we use the `adf.test()` function in the `tseries` package, which implements the Augmented Dickey-Fuller Test. This statistic tests the null hypothesis that the time series is non-stationary. Thus, we will conclude that a time series is stationary if the p-value  $< 0.05$ .

```
adf.raw <- adf.test(abund.ts, alternative = "stationary")
adf.raw$p.value
```

```
## [1] 0.3229509
```

The Dickey-Fuller test indicates that our time series does not meet the assumption of stationarity. Let’s try differencing the time series using the `diff()` function, which will create a new time series where  $Y_d = Y_t - Y_{t-1}$ . After re-running the Dickey-Fuller test, we can see that the differencing helped us meet the assumptions of stationarity.

```
abund.ts.diff <- diff(abund.ts)
adf.diff <- adf.test(abund.ts.diff, alternative = "stationary")
adf.diff$p.value
```

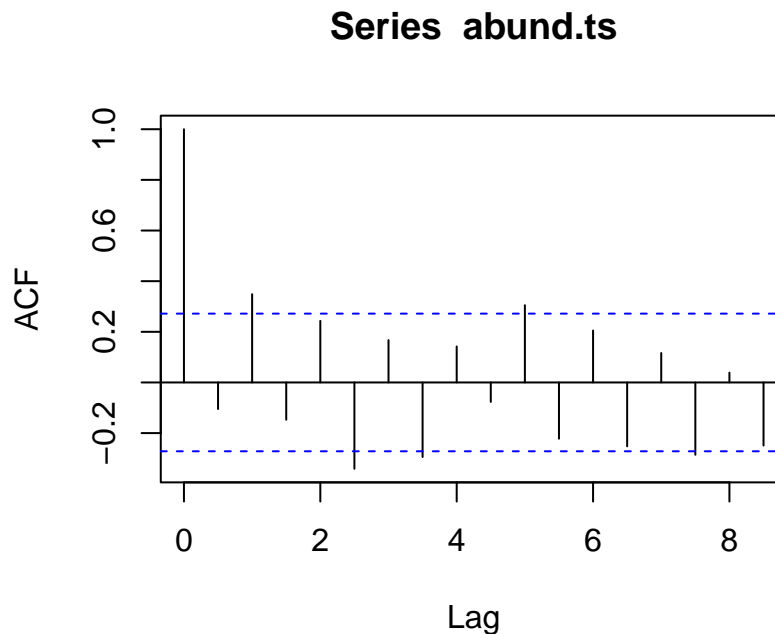
```
## [1] 0.02186602
```



```
#plot.ts(abund.ts.diff, ylab = "Rodent Abundance (#/hectare)", xlab = "Time (year)", las = 1)
```

The next step in the ARMA pipeline is to look at the lags in our time series using the **autocorrelation function (ACF)**. These plots help us visualize structure in our data, while informing the parameterization of our ARMA models. Specifically, the ACF tells us about the lags of the forecast errors and thus provides information for the moving average (MA) component of the model. The ACF simply looks at the correlation between lagged intervals in the time series. When lag = 0, ACF will always equal 1. After that, we expect the ACF to decline with increasing time lag. If we see that there is a significant correlation at a given lag (i.e., when a correlation exceeds the horizontal dashed lines), this information can be used to parameterize our AMRA models. For example, in the non-differenced time series we see that there is a significant positive correlation at lag = 2. Recall, the frequency of our data divides the year up into rainy and non-rainy season. So the lag = 2 correlation could be reflecting autocorrelation of error terms on an annual cycle.

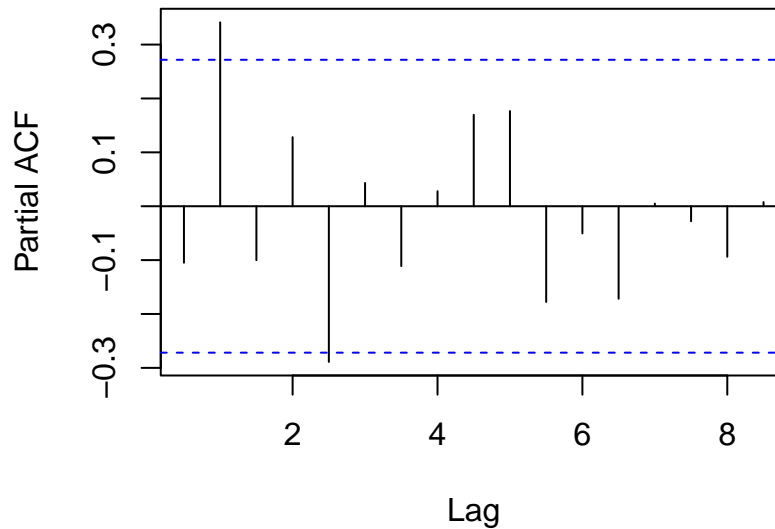
```
acf(abund.ts)
```



We also look at the time series using the **partial autocorrelation function (PACF)**. PACF calculates correlations between two series after correcting for correlation that might exist with another lagged series. In contrast to the ACF, significant partial correlation coefficients tell us about lags that can be addressed with the autoregressive (AR) component of the ARMA model. In the following PACF, we can see that there is a significant partial correlation at lag = 2 and lag = 5.

```
pacf(abund.ts)
```

## Series abund.ts

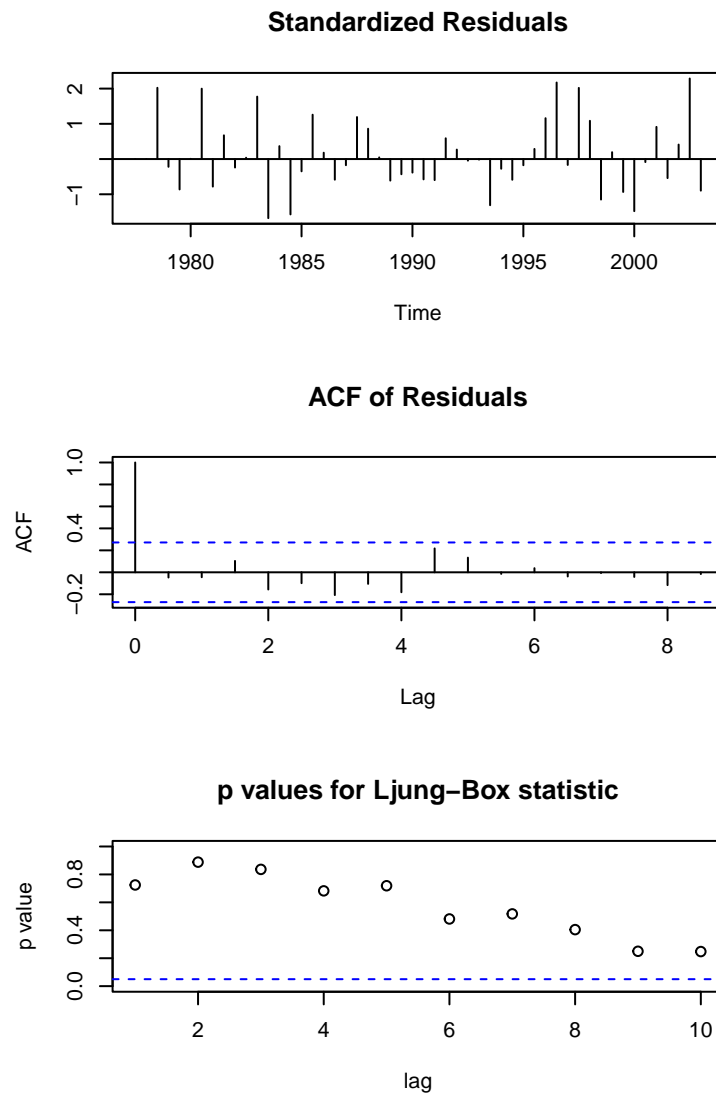


With this information in hand, let's try to arrive at our final ARMA model. Because we found that differencing helped us meet the assumption of stationarity, we are actually going to use an auto-regressive *integrated* moving average (ARIMA) model. ARIMA models accept parameters  $p$ ,  $d$ , and  $q$ , which describe the number of autoregressive lags (inferred from PACF), differencing, and order of the moving-average model (inferred from ACF), respectively. We are going to use the function `auto.arima` from the `forecast` package to identify the best ARIMA model based on information criteria (AIC, AICc, and BIC). This function is particularly useful because we have some complexities related to the effects of seasonality. After identifying the ARIMA model, we can look at the diagnostics using `tsdiag` and then make forecasts about rodent densities into the future using the `predict()` function from the `arima` package.

```
abund.arm <- auto.arima(abund.ts)
abund.arm <- arima((abund.ts), c(0, 0, 1), seasonal = list(order = c(2, 1, 0),
  period = 2), include.mean = TRUE)
```

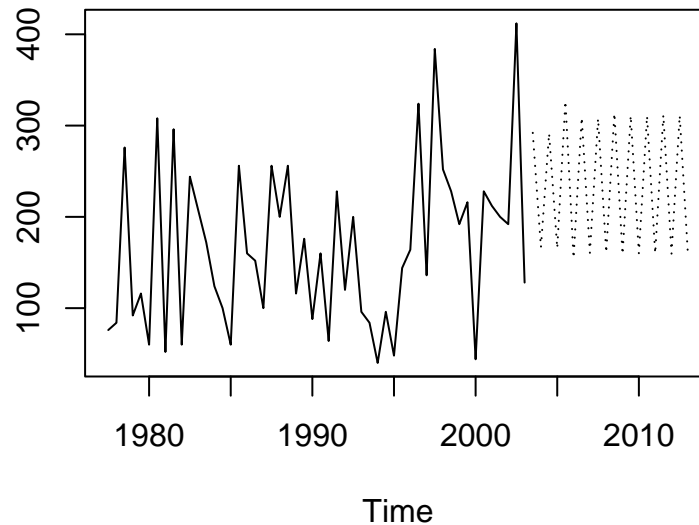
Let's look at some diagnostic plots for the ARIMA model

```
tsdiag(abund.arm)
```



Finally, let's use predictions from the model to forecast future rodent abundances in the study plot:

```
pred.arm <- predict(abund.arm, n.ahead = 20)
ts.plot(abund.ts, pred.arm$pred, lty = c(1,3))
```



## 5) REPEATED MEASURES ANALYSIS OF VARIANCE (RM-ANOVA)

When scientists go to the trouble to set up an elaborate experiment, there is a natural tendency to take more than a single measurement on a subject (i.e., experimental unit). This is true for laboratory and field studies in ecology and evolution, but is also common in other fields such as medicine, psychology, and the social sciences. Studies that take repeated measurements on a subject are referred to as **longitudinal designs**. It is important to emphasize that repeated observations on a subject are non-independent. Independence is a critical assumption of most parametric statistics, like analysis of variance (ANOVA). RM-ANOVA explicitly accounts for this non-independence and allows one to test for the main effects of time and treatment along with the time x treatment interaction.

In the following section, we perform and interpret an RM-ANOVA using richness data from the Portal Project.

### Wrangle data for RM-ANOVA

In the following R chunk, we calculate richness over time from two of the Portal plots. The first treatment is the “Control” where rodents are free to move in and out of plots. The second treatment is the “Rodent Exclosure”, which attempts to exclude all rodents. To create the necessary data frame, we use `dplyr` to construct a time-by-species matrix. We use `count()` to sum the number of individuals belonging to each taxon while maintaining the grouping by year, plot\_id, and plot\_type. We use the `spread()` function from `tidyr` on the split dataset to convert parts of a long format dataset to a wide format dataset. Last, we calculate richness (i.e., number of taxon per plot per year) for each replicate in the two treatments.

```
# Construct time-by-species matrix
time.by.species <- group_by(portal, year, plot_id,
  plot_type) %>% count(taxon) %>% spread(key = taxon, value = n, fill = 0)

# Calculate observed richness from time-by-species matrix
richness <- as.data.frame(rowSums(time.by.species[, -c(1:3)] > 0))

# Create data frame with experimental design and richness data
rich.all <- data.frame(time.by.species[, 1:3, ], richness)

# Rename column
names(rich.all)[4] <- "richness"
```

```
# Pull out two of the five Portal treatments
rich.treat <- rich.all[which(rich.all$plot_type ==
  "Control" | rich.all$plot_type == "Rodent Exclosure"), ]
```

## Plot data

While the base package in R can make beautiful plots and has tremendous flexibility, it can also require a lot of effort to generate figures. Another, way to make figures in R is with the package `ggplot`. As you will see, with relatively few lines of code, we can make a nice-looking figure with `ggplot` showing the effects of rodent exclosure on rodent richness. But first, we need to calculate some summary statistics for the plotting. Again, we use the `group_by` function from `dplyr` along with pipes to retrieve the mean and standard error of the mean (SEM) using the `summarise` function.

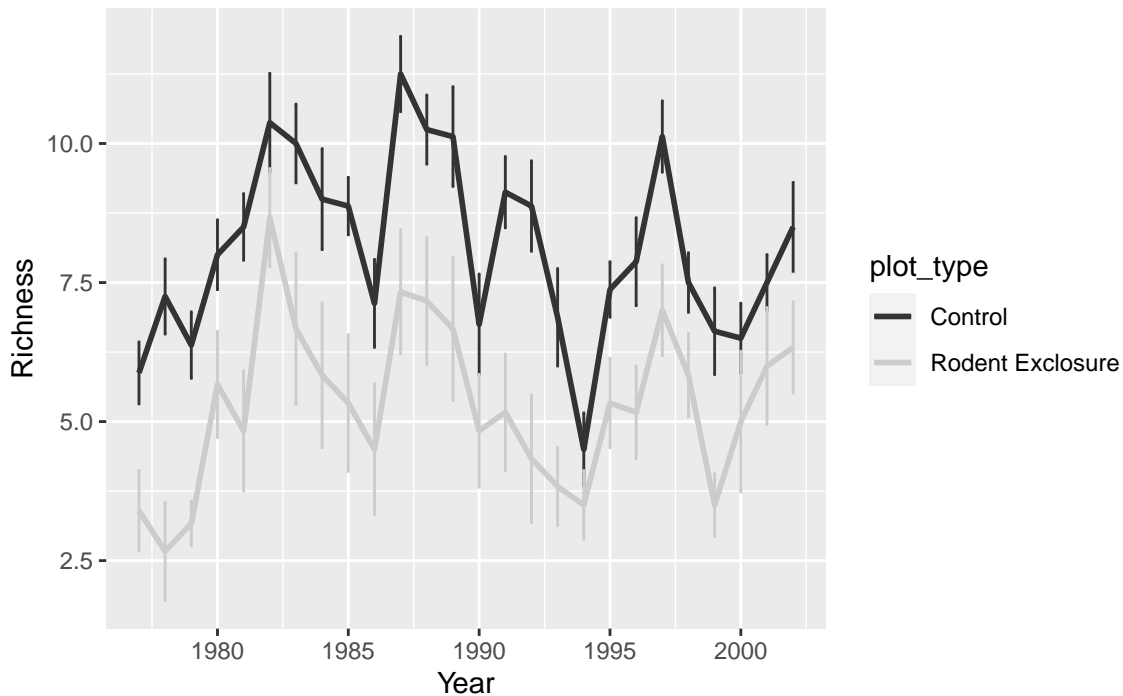
```
rich.treat.plot <- group_by(rich.treat, plot_type, year) %>%
  summarise(
    mean = mean(richness),    # avg. richness per group
    sd = sd(richness),        # stand. dev. per group
    n = n(),                  # num. obs. per group
    sem = sd/sqrt(n)          # calc. std. err. mean.
```

```
## 'summarise()' has grouped output by 'plot_type'. You can override using the
## '.groups' argument.
```

```
rich.plot <- ggplot(rich.treat.plot, aes(x = year, y = mean, color = plot_type)) +
  geom_line(size = 1, show.legend = T) +
  geom_errorbar(aes(ymin = mean - sem, ymax = mean + sem), width = .1) +
  xlim(1977, 2002) +
  xlab("Year") +
  ylab("Richness")+
  scale_color_grey()
```

```
## Warning: Using 'size' aesthetic for lines was deprecated in ggplot2 3.4.0.
## i Please use 'linewidth' instead.
## This warning is displayed once every 8 hours.
## Call 'lifecycle::last_lifecycle_warnings()' to see where this warning was
## generated.
```

```
plot(rich.plot)
```



## Perform RM-ANOVA

Based on our plot, it appears that rodent richness changes quite a bit from year to year. The plot also suggests that the enclosure treatment reduced rodent richness. Let's perform a RM-ANOVA to see whether statistics match up with our observations. We will implement RM-ANOVA using the “linear and non-linear mixed-effects models” package in R (i.e., `nlme`). **Mixed effects** refers to models that contain both fixed and random effects. The fixed effects in our analysis are time and treatment; these are aspects of the design that were under the researchers' control. In contrast, within plot (i.e., subject) variation is considered a random effect. RM-ANOVA quantifies model error based on the variance of observations within and between subjects. In the R chunk below, we implement RM-ANOVA with the `lme()` function to test for the effects of treatment (i.e., “plot\_type”), time (i.e., year), and a treatment  $\times$  time interaction on rodent richness. The random statement indicates that plot\_id is a random variable that will be assigned its own intercept. In addition, the correlation statement specifies the covariance structure that is associated with the repeated measures. Here, we use an autoregressive process of order 1, which means that an observation at time  $t$  will be most influenced by observations at time  $t-1$ . Alternate covariance structures to consider in an RM-ANOVA are “unstructured” and “compound symmetry”.

```
rich.rm <- lme(richness ~ plot_type * year, random = ~ 1 | plot_id,
              correlation = corAR1(form = ~ 1 | plot_id),
              data = rich.treat)

# Look at detailed output
summary(rich.rm)

# Obtain F-test
anova(rich.rm)

# Make cleaner ANOVA table
set.caption("RMANOVA for Portal")
pander(anova(rich.rm))
```

```
# Use `lsmeans` package for time-corrected marginal means
lsmeans(rich.rm, ~plot_type)
```

## 6) TEMPORAL BETA DIVERSITY

As we have learned this semester,  $\beta$ -diversity examines biodiversity among samples. In previous weeks, we have emphasized features of  $\beta$ -diversity that relate to the distribution of species and samples in space. Now we will explore temporal dimensions of  $\beta$ -diversity by examining changes in the abundance or presence-absence of species over time. Specifically, we introduce concepts and measures of turnover, rank shift, and rank change interval.

Let's revisit the figure of annual rodent richness over time. RM-ANOVA revealed that exclosure led to 70% reduction in rodent richness. Although there was no significant effect of time in the RM-ANOVA model, rodent richness fluctuates with discernable peaks in 1982, 1987, 1992, 1997, and 2002. Interestingly, the interannual trends in richness are similar across treatments. We will investigate these patterns in the context of temporal biodiversity in the following sections.

### A. Turnover

The temporal pattern of annual richness could be explained in part by changes in species composition over time (i.e., species turnover). Low turnover means that composition is relatively stable through time, while high turnover reflects dynamic community structure. Turnover can be driven by the introduction and establishment of new species or the loss of a resident species. These gains and losses of species can reflect a suite of eco-evolutionary processes including natural immigration, invasion by exotic species, disease outbreaks, and competitive exclusion. Here, we calculate the overall turnover with a simple equation:

$$\text{Total turnover} = \frac{\text{species gained} + \text{species lost}}{\text{total species in both timepoints}}$$

In the following R chunks, we use the `codyn` package (Hallett et al. 2016), which calculates a number of metrics to analyze community dynamics, including turnover.

```
# First, calculate the species abundances from each site over time
portal.species.abunds <- group_by(portal, year, plot_type) %>% count(taxon)
```

```
# Calculate total turnover
portal.total <- turnover(df = portal.species.abunds,
  time.var = "year",
  species.var = "taxon",
  abundance.var = "n",
  replicate.var = "plot_type",
  metric = "total")
```

```
# Calculate species gained
portal.appearance <- turnover(df = portal.species.abunds,
  time.var = "year",
  species.var = "taxon",
  abundance.var = "n",
  replicate.var = "plot_type",
  metric = "appearance")
```

```
# Calculate species lost
portal.disappearance <- turnover(df = portal.species.abunds,
                                time.var = "year",
                                species.var = "taxon",
                                abundance.var = "n",
                                replicate.var = "plot_type",
                                metric = "disappearance")
```

Each of these objects contains a column for the value of the turnover metric (total, appearance, disappearance), the second year in the pairwise comparison, and the type of plot (i.e., treatment). For easier plotting, let's combine these turnover metrics into a single data table:

```
# Use `join()` from `dplyr` to join the columns by shared year & plot type columns
portal.turnover <- full_join(portal.total, portal.disappearance) %>%
  full_join(portal.appearance)
```

```
## Joining with 'by = join_by(year, plot_type)'
## Joining with 'by = join_by(year, plot_type)'
```

```
# Use `gather()` from `tidyr` to convert back to long-form
portal.turnover <- gather(portal.turnover, key = metric, value = turnover,
                           total, appearance, disappearance)
```

In the R code chunk above, we did a lot of data wrangling using only a couple lines of code. Take a moment to reflect on this. We had three separate data frames containing different turnover metrics. But those metrics referred to the same plots and years. So, we joined them together using their shared year and plot\_type index to create a single data-table. We first joined the total and disappearance values, then piped (%>%) this joined data-table to be the first argument in another join function. Try running each of these full\_join() statements separately to see what is happening at each step.

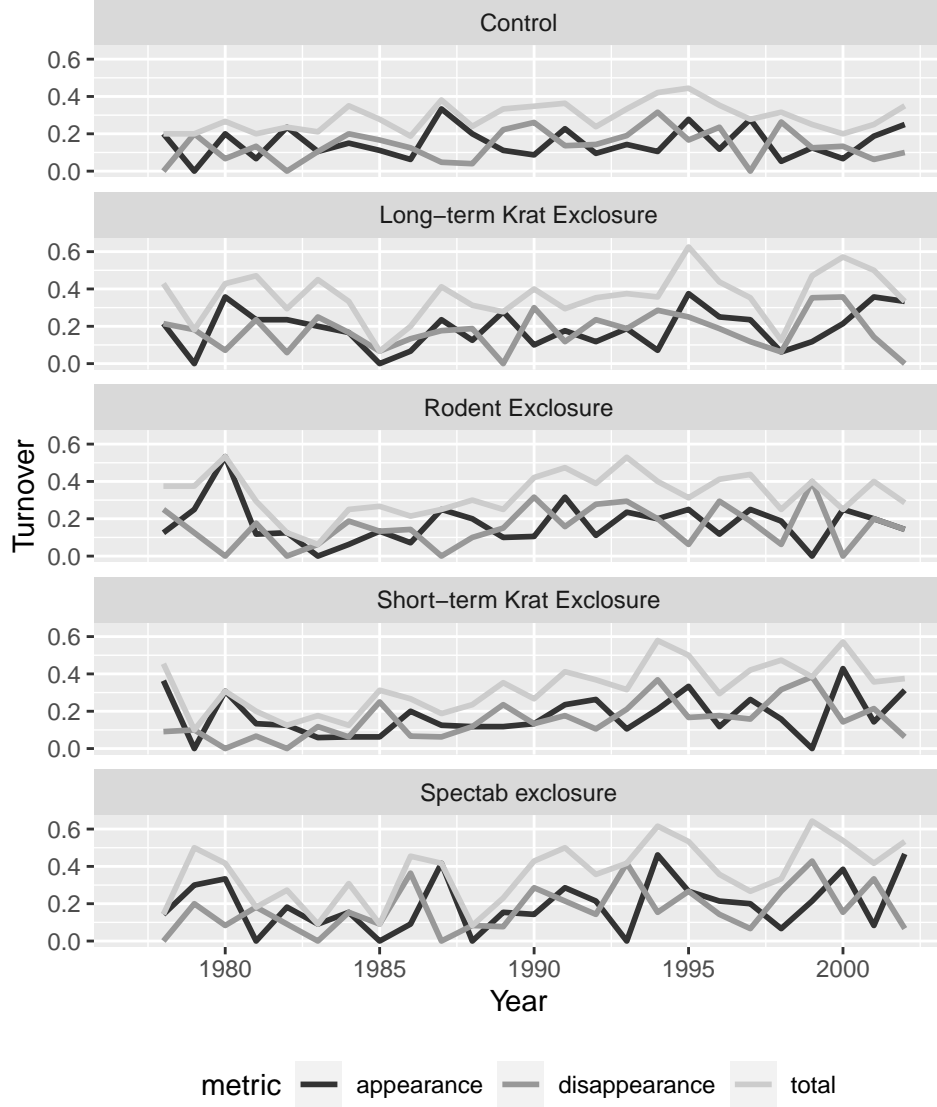
Next, we turned the wide-form data table back into a long-form table to facilitate plotting. We did this using the gather() function. Essentially, this function takes portal.turnover and creates a new column of keys and calls it “metric”. It then creates another new column of associated values and calls it “turnover”. The keys in the metric column are the old columns we gathered together (i.e., total, appearance, disappearance). The values that go in turnover are the values that were previously in the total, appearance, disappearance columns.

Take a look at our new data table with the three different turnover metrics calculated for each year and treatment. Try this using View(portal.turnover).

Now, let's use ggplot to visualize the turnover metrics in all five of the Portal treatments over the entire annual time series.

```
turn.plot <- ggplot(
  portal.turnover, aes(x = year, y = turnover, color = metric)) +
  geom_line(size = 1, show.legend = T) +
  facet_wrap(~plot_type, ncol = 1) +
  xlim(1977, 2002) +
  xlab("Year") +
  ylab("Turnover") +
  theme(legend.position = "bottom") +
  scale_color_grey()
plot(turn.plot)
```





## B. Rank Shift

Turnover estimates place equal weight on the gain and loss of a species irrespective of its abundance. However, the gain or loss of a common vs. rare species may have important implications for species interactions and ecosystem functioning. For example, the “mass ratio theory” (Grime 1998) states that species should contribute to community processes in proportion to their abundance. However, more recent studies suggest that rare species contribute disproportionately to community processes (Leitao et al. 2016). In this section, we introduce a  $\beta$ -diversity metric called **mean rank shift (MRS)** (Collins et al. 2008) that allows us to calculate the shift in ranks using the following equation:

$$MRS = \sum_{i=1}^n (|R_{i,t+1} - R_{i,t}|) / n$$

where  $R_i$  is the rank of a species found in samples at time  $t$  and time  $t + 1$ . MRS then sums the absolute value of the rank changes for  $n$  species that are shared between samples. Thus, the higher the MRS index, the more change there is in the commonness and rarity of taxa. In the following R chunk, we calculate MRS

from `portal.rankshift` which is the abundance of species in each site over time (see above). We then plot MRS and characterize its variability.

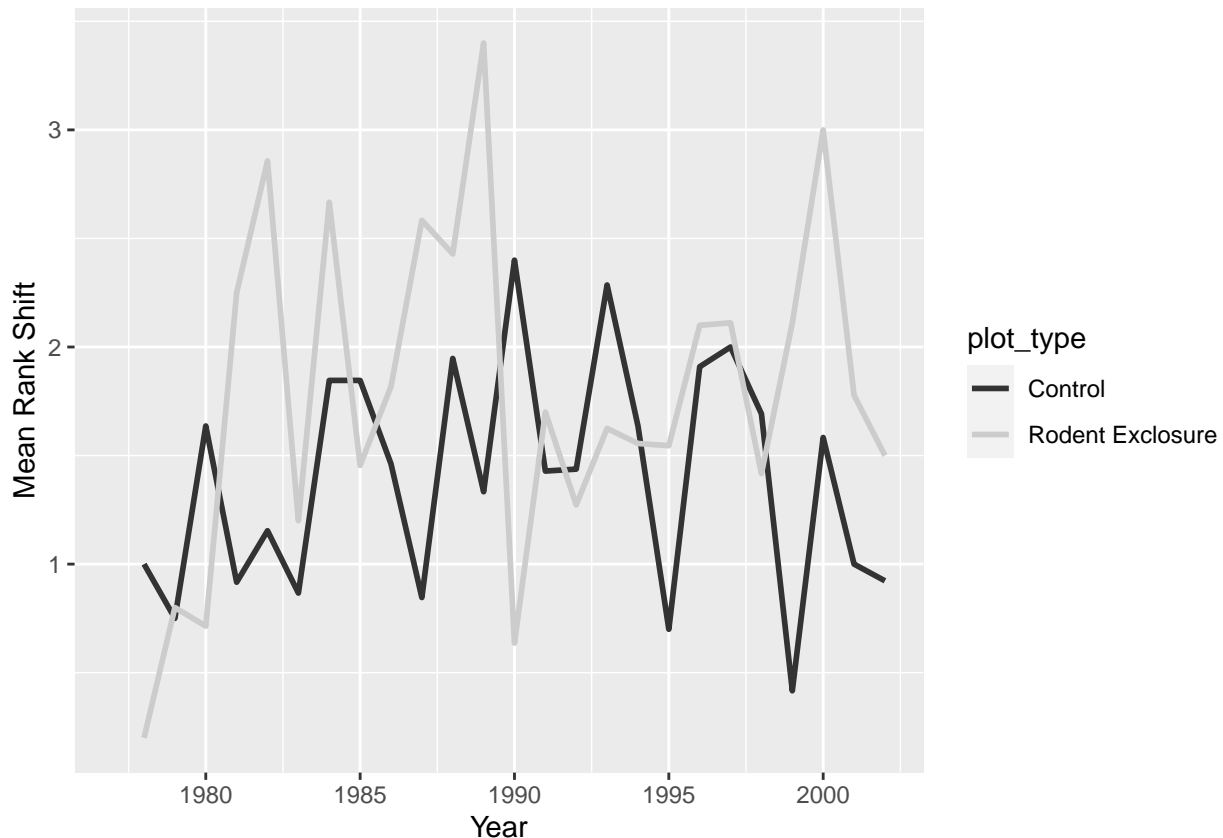
```
# Pull out the two treatments we analyzed earlier
portal.abunds.cont.rodent <- filter(portal.species.abunds,
  plot_type == "Control" | plot_type == "Rodent Enclosure")

# Calculate MRS
portal.rankshift <- rank_shift(
  df = as.data.frame(portal.abunds.cont.rodent),
  time.var = "year",
  species.var = "taxon",
  abundance.var = "n",
  replicate.var = "plot_type")

# Replace the year range with a single value to plot
portal.rankshift$year <- as.numeric(substr(portal.rankshift$year_pair, 6, 9))

# Create ggplot
rankshift.plot <- ggplot(portal.rankshift, aes(x = year, y = MRS, color = plot_type)) +
  geom_line(size = 1) +
  xlim(1977, 2002) +
  xlab("Year") +
  ylab("Mean Rank Shift") +
  scale_color_grey()

plot(rankshift.plot)
```



```
# Does one plot type show higher or lower MRS, on average?
group_by(portal.rankshift, plot_type) %>%
  summarise(
    mean = mean(MRS),
    cv = sd(MRS)/mean)
```

```
## # A tibble: 2 x 3
##   plot_type      mean    cv
##   <chr>      <dbl> <dbl>
## 1 Control      1.40 0.376
## 2 Rodent Exclosure 1.79 0.436
```

### C. Rate Change Interval

How much can communities diverge over time? And how fast does this happen? These are important basic questions, but are also important for restoration where legacy effects often impede management practices. For example, in highly dynamic systems, turnover may quickly saturate at a high level, while in more stable communities, it may take decades or centuries for communities to reach a similar level of dissimilarity, if they ever do. In the following section, we use the `codyn` package to calculate the **rate change interval** for species abundances in the Portal site and plot this information using `ggplot`.

If we take a look at `help(rate_change_interval)`, we see that this function calculates the Euclidean distance between two communities. Remember from our discussion of  $\beta$ -diversity, that Euclidean distances are not appropriate for calculating community dissimilarity because the distance between sites that share no species in common may be shorter than between sites that share species but in different abundances! So, we need to appropriately transform the data before drawing any conclusions. Recall that one attractive transformation is the Hellinger transformation (see Legendre and Gallagher 2001). The Euclidean distance calculated on the Hellinger-transformed species abundances generates the Hellinger distance.

The Hellinger transformation is the square root of the relative abundances:  $y'_{ij} = \sqrt{\frac{y_{ij}}{y_{i+}}}$

```
# In order to calculate relative abundances, we need total abundances
# Let's add a column for total abundances
# We will relativize species abundances across the whole dataset so
# the transformed distances are preserved
portal.species.abunds$tot.abund <- rep(sum(portal.species.abunds$n),
                                       length(portal.species.abunds$n))

# Now, apply Hellinger transformation
portal.hellinger.transf <- portal.species.abunds %>%
  mutate(hellinger.transf = sqrt(n / tot.abund))

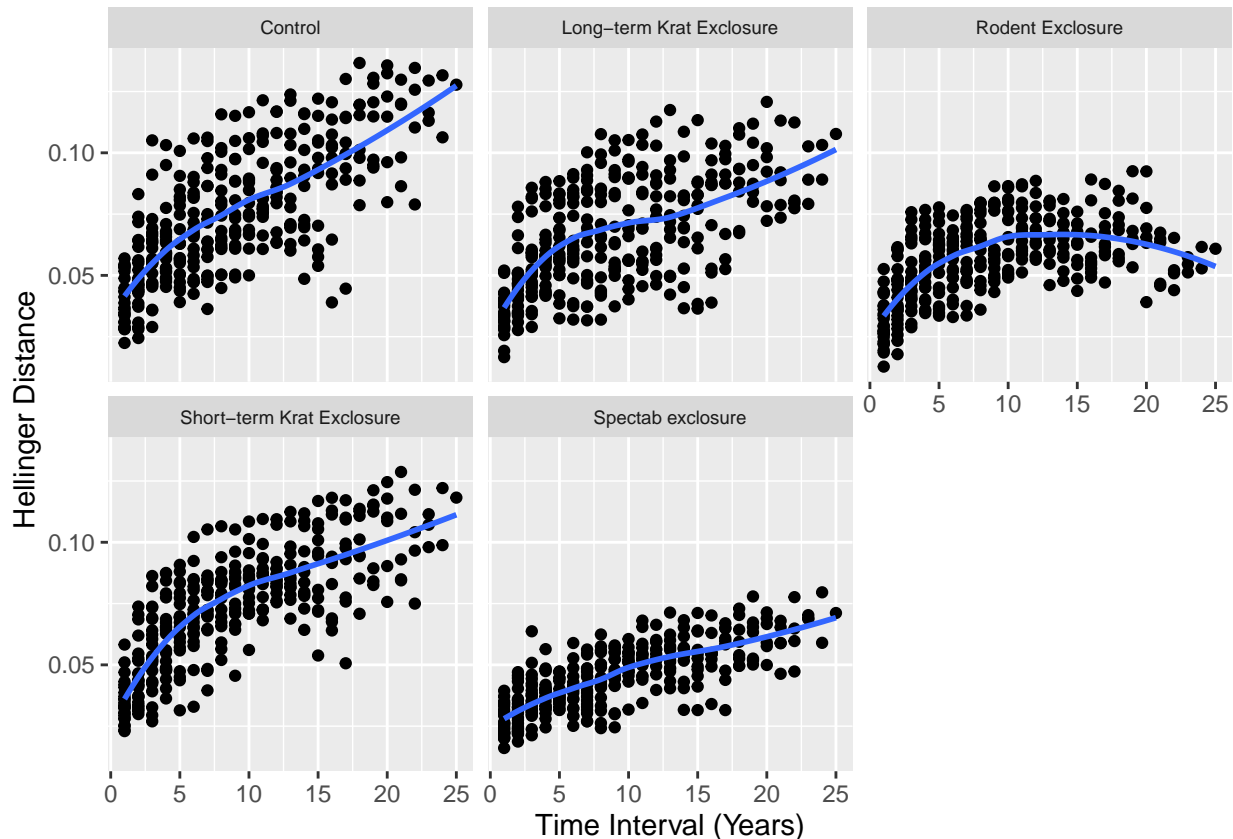
# The mutate function creates a new column "hellinger.transf"
# by taking the square root of species relative abundance

# We can use this new column as our "abundance" vector
portal.change.int <- rate_change_interval(portal.hellinger.transf,
    time.var = "year",
    species.var = "taxon",
    abundance.var = "hellinger.transf",
    replicate.var = "plot_type")

rate.plot <- ggplot(portal.change.int, aes(interval, distance)) +
```

```
geom_point() +
facet_wrap(~plot_type) +
theme(strip.text.x = element_text(size = 7)) +
stat_smooth(method = "loess", se = F, size = 1) +
ylab("Hellinger Distance") +
xlab("Time Interval (Years)")
rate.plot
```

```
## 'geom_smooth()' using formula = 'y ~ x'
```



## 7) STABILITY

The stability of ecological systems has been at the forefront of ecological research for decades (Ives and Carpenter 2007). There are many definitions of stability, and these are beyond the scope of this course (but see Pimm 1984, Grimm et al. 1997). In mathematical models, notions of stability often revolve around responses to perturbations and whether these perturbations grow away from or return to a stable equilibrium, but applying these ideas to real datasets is often less straightforward. Another way to think about stability is the lack of variability in some value (e.g., community biomass, population densities, etc.). Stability can be analyzed with respect to the individual species that make up a community (i.e., compositional variability), or some measure that integrates across species (i.e., aggregate variability), such as total biomass, total abundance, or richness (Micheli et al. 1999). Understanding how species diversity relates to measures of stability is still a highly active area of research (McCann 2000), but some general trends seem to be that increasing diversity decreases the stability of populations but increases aggregate measures of stability (e.g., biomass) (Tilman 1999). Below, we explore some metrics that have been used to analyze empirical data to address questions related to ecological stability.

## A. Community Stability

The stability of an aggregate measure of an ecological system can be assessed by measuring its variability. One way to characterize variability is the Coefficient of Variation (CV). The CV relativizes the standard deviation of a variable to its mean value because variance scales with the mean. By using the CV, we can more easily compare the variability of systems with different mean values. We can calculate the CV as follows:

$$CV = \frac{\sigma}{\mu}$$

where  $\sigma$  is the standard deviation and  $\mu$  is the mean value.

Higher CV indicates more variability, and lower CV indicates less variability. Therefore, we can measure stability as the inverse of CV:

$$\text{Stability} = \frac{1}{CV}$$

Let's calculate stability within each plot type now.

```
portal.stab <- community_stability(df = as.data.frame(portal.species.abunds),  
  time.var = "year",  
  abundance.var = "n",  
  replicate.var = "plot_type")  
pander(portal.stab)
```

plot_type	stability
Control	3.044
Long-term Krat Exclosure	1.865
Rodent Exclosure	1.864
Short-term Krat Exclosure	2.462
Spectab exclosure	2.911

## B. Species Synchrony

One potential mechanism underlying stability is synchrony. Species synchrony is a measure of whether population densities fluctuate independently or not, and if not, how strongly they positively or negatively covary. When species exhibit strong synchrony, species densities positively covary. This suggests that species respond similarly to changes in the environment, and has been hypothesized to be a key driver of instability. For example, if all species decline together, a single disturbance event could be severely destabilizing. When species display strong asynchrony, species densities negatively covary. This suggests that species respond differently to changes in the environment, which has been hypothesized to stabilize aggregate community metrics. In this case, some species can compensate in density for the losses of other species, a phenomenon called compensatory dynamics (Gonzalez and Loreau 2009).

Here, we will calculate two measures of community-wide synchrony that range from  $-1$  for perfect asynchrony to  $+1$  for perfect synchrony. Loreau and de Mazancourt (2008) describe a synchrony metric that compares aggregate community variance to population-level variance. Gross et al. (2014) present a different metric, which compares average species-level correlations with the aggregate community. See the derivations in the original papers for more detail.

```
portal.loreau <- synchrony(df = as.data.frame(portal.species.abunds),  
  time.var = "year",  
  species.var = "taxon",  
  abundance.var = "n",
```

```

    replicate.var = "plot_type",
    metric = "Loreau")
names(portal.loreau)[2] <- "loreau"

portal.gross <- synchrony(df = as.data.frame(portal.species.abunds),
    time.var = "year",
    species.var = "taxon",
    abundance.var = "n",
    replicate.var = "plot_type",
    metric = "Gross")
names(portal.gross)[2] <- "gross"

pander(full_join(portal.loreau, portal.gross))

```

```
## Joining with 'by = join_by(plot_type)'
```

plot_type	loreau	gross
Control	0.1869	0.1263
Long-term Krat Exclosure	0.1578	0.07418
Rodent Exclosure	0.187	0.1423
Short-term Krat Exclosure	0.08773	0.001546
Spectab exclosure	0.1542	0.1393

The synchrony values are all positive, but pretty far from 1, suggesting there is probably not strong positive synchrony at these temporal and spatial scales.

### C. Variance Ratio

Similar to concepts of community-wide synchrony, here we present another metric, the variance ratio (VR) (Schluter 1984). The VR allows us to test for positive or negative species covariance and is often used to detect compensatory dynamics. VR is the ratio of the variance in aggregate abundances to the sum of variances of individual species. Let's look at the numerator first ( $\text{Var}(N)$ ). When there is no or little variation in total number of individuals over time, the numerator is close to zero. This suggests that no matter how individual species fluctuate, their fluctuations compensate for one another, resulting in a relatively stable total abundance. This is an indication of negative covariance (asynchrony) in species abundances. Alternatively, when species positively covary (i.e., they are synchronous), their individual fluctuations become amplified when looking at the total abundance (because there is no compensation). Consequently, the numerator becomes much larger than the denominator. Thus, we can summarise this as follows: when  $\text{VR} = 1$  species do not covary; when  $\text{VR} > 1$ , species positively covary; and when  $\text{VR} < 1$  species negatively covary. To test for significance, we will compare the observed variance ratio to a distribution of ratios calculated from randomized null communities.

```

portal.vr <- variance_ratio(df = as.data.frame(portal.species.abunds),
    time.var = "year", species.var = "taxon",
    abundance.var = "n", replicate.var = "plot_type",
    bootnumber = 1000, average.replicates = T,
    level = 0.95)
pander(portal.vr)

```

lowerCI	upperCI	nullmean	VR
0.6845	1.383	1.005	1.325

From the Portal data, we calculate a VR of  $\sim 1.3$ . This value is greater than 1, suggesting positive covariation among species. However, we also note that the confidence intervals (based on null matrix randomization) bracket 1. In general, this result agrees with the synchrony calculations, suggesting there is weak, positive covariation among species that may respond to environmental variability (e.g., drought, fire) in similar ways.

#### D. Biodiversity-Stability Relationships

As suggested above, species diversity may affect the functioning and stability of community properties. It is generally thought that more diverse ecosystems are more stable. Often these ideas are tested experimentally where species richness is directly manipulated. But in this section, let's see whether portal data are consistent with expectation from biodiversity-stability theory.

```
# Recall, earlier we calculated richness in each plot type in each year
# Let's group only by plot_id
# Then, we we summarise average annual richness in each plot type
portal.mean.rich.plot <- rich.all %>%
  group_by(plot_id) %>%
  summarise(mean.rich = mean(richness))

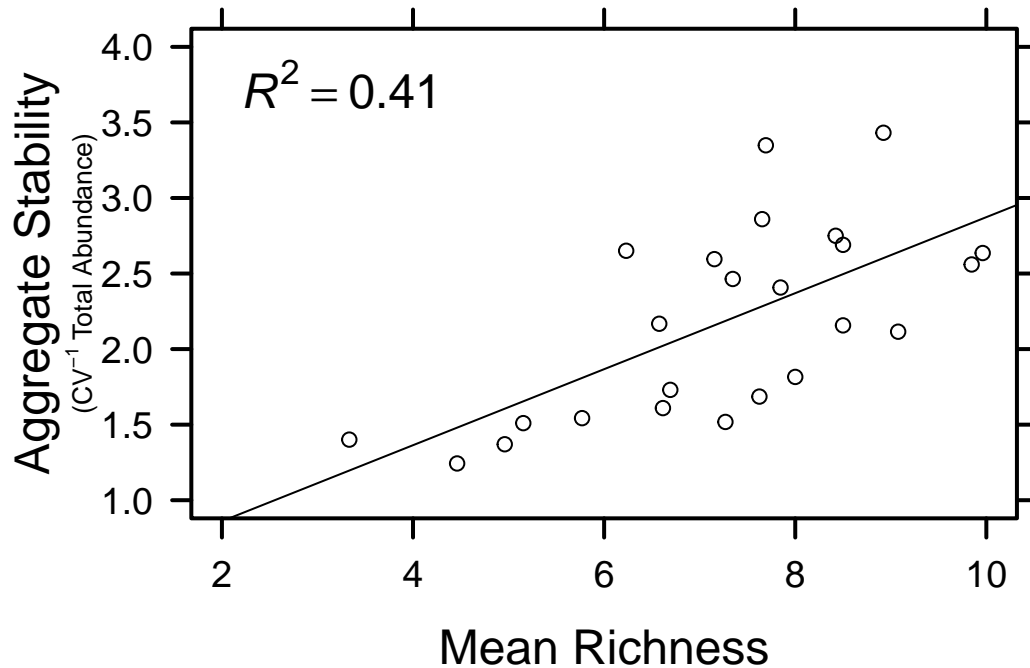
# Let's take a look at how stability metrics relate to mean richness
portal.plot.abunds <- as.data.frame(
  group_by(portal, year, plot_id) %>% count(taxon))
portal.stab.plot <- community_stability(df = portal.plot.abunds,
  time.var = "year",
  abundance.var = "n",
  replicate.var = "plot_id")

# Join richness and stability
portal.div.stab <- portal.mean.rich.plot %>%
  inner_join(portal.stab.plot)
```

```
## Joining with 'by = join_by(plot_id)'
```

```
# Plot the relationship
par(mar = c(5,5,1,1))
plot(portal.div.stab$stability ~ portal.div.stab$mean.rich,
  xlab = "", ylab = "", yaxt = "n", xaxt = "n",
  xlim = c(2,10), ylim = c(1,4))
axis(side = 1, cex.axis = 1.2, lwd.ticks = 2, las = 1)
axis(side = 2, cex.axis = 1.2, lwd.ticks = 2, las = 1)
axis(side = 3, lwd.ticks = 2, las = 1, labels = F)
axis(side = 4, lwd.ticks = 2, las = 1, labels = F)
box(lwd = 2)
mtext("Mean Richness", side = 1, line = 3, cex = 1.5)
mtext("Aggregate Stability", side = 2, line = 3.5, cex = 1.5)
mtext(expression(paste("(CV"-1," Total Abundance)")),
  side = 2, line = 2.25, cex = .8)
```

```
div.stab.lm <- lm(portal.div.stab$stability ~ portal.div.stab$mean.rich)
abline(div.stab.lm)
r2 <- bquote(italic(R)^2 == .(format(
  summary(div.stab.lm)$adj.r.square, digits = 3)))
text(3.25,3.75, cex = 1.5, labels = r2)
```



## REFERENCES

- Collins, S. L., K. N. Suding, E. E. Cleland, M. Batty, S. C. Pennings, K. L. Gross, J. B. Grace et al. 2008. Rank clocks and plant community dynamics. *Ecology* 89:3534-3541.
- de Mazancourt, C., F. Isbell, A. Larocque, F. Berendse, E. De Luca, J. B. Grace, B. Haegeman et al. 2013. Predicting ecosystem stability from community composition and biodiversity. *Ecology Letters* 16:617-625.
- Gonzalez, A., and M. Loreau. 2009. The causes and consequences of compensatory dynamics in ecological communities. *Annual Review of Ecology, Evolution, and Systematics* 40:393-414.
- Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86:902-910.
- Grimm, V., and C. Wissel. 1997. Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* 109:323-334.
- Gross, K., B. J. Cardinale, J. W. Fox, A. Gonzalez, M. Loreau, H. W. Polley, P. B. Reich et al. 2014. Species richness and the temporal stability of biomass production: a new analysis of recent biodiversity experiments. *The American Naturalist* 183:1-12.
- Hallett, L. M., S. K. Jones, A. A. M. MacDonald, M. B. Jones, D. F. B. Flynn, J. Ripplinger, P. Slaughter et al. 2016. codyn: An r package of community dynamics metrics. *Methods in Ecology and Evolution* 7:1146-1151.
- Ives, A. R., and S. R. Carpenter. 2007. Stability and diversity of ecosystems. *Science* 317:58-62.
- Legendre, P., and E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129:271-280.



- Leitão, R. P., J. Zuanon, S. Villéger, S. E. Williams, C. Baraloto, C. Fortunel, F. P. Mendonça et al. 2016. Rare species contribute disproportionately to the functional structure of species assemblages. *Proceedings of the Royal Society B: Biological Sciences* 283.
- Loreau, M., and C. de Mazancourt. 2008. Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *The American Naturalist* 172:E48-E66.
- McCann, K. S. 2000. The diversity-stability debate. *Nature* 405:228-233.
- Micheli, F., K. L. Cottingham, J. Bascompte, O. N. Bjørnstad, G. L. Eckert, J. M. Fischer, T. H. Keitt et al. 1999. The dual nature of community variability. *Oikos* 85:161-169.
- Pimm, S. L. 1984. The complexity and stability of ecosystems. *Nature* 307:321-326.
- Schluter, D. 1984. A variance ratio test for detecting species associations, with some applications. *Ecology* 65:998-1005.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80:1455-1474.