Biodiversity and Ecosystem Function

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"Over the last two decades, empirical work has established that higher biodiversity can lead to greater primary productivity; however, the importance of different aspects of biodiversity in contributing to such relationships is rarely elucidated" (**Gorssman et al. 2017**).

The are a number of metrics that quantify the biodiversity-ecosystem funtioning and the most common the effect of biodiversity on plant productivity in terms of 'relative yield' – i.e. the ratio of species-level productivity observed in a multi-species mixture, relative to that in monoculture. Observed relative yield is then compared to a expected relative yield, in which the relative yield is proportional to the initial relative species abundance. Then, if the observed exceeds the expected, one can conclude that productivity per unit area is higher in mixtures than in average monocultures.

A major advantage of 'relative yield' related metrics is that one can partition them into different components and then use these components to summarize different characteristics of the relationship between biodiversity and ecosystem functioning (**Loreau & Hector, 2001, Isbell et al., 2018**). The most common used of these metrics, is the *Loreau and Hector partition* that groups deviations between observed and expected yield into two components: the *'selection effect'* and the *'complementarity effect'* (**Loreau & Hector, 2001**). In *selection effect*, the presence of highly productive species species is responsible for higher productivity with greater diversity (**Aarssen 1997, Gorssman et al. 2017**). In other words, the biodiversity-productive relationship emerge just because sample plots have highly productive species (irrespective of plot diversity), and that the most productive species had more chance (*to be sampled*) of being included in the more diverse plots than in the less diverse plots. In *complementary effect*, complementary interaction between species related to functional differences are driving the biodiversity-productivity relationship (**Loreau & Hector, 2001, Gorssman et al. 2017**).

In this lab, we will explore some questions about biodiversity and its effects on ecosystem functioning. To do so, we will use data and scripts (with some modifications) kindly provided by Jake Gorssman. We will assess the relative importance of species richness, phylogenetic diversity, functional diversity, and identity of neighbors for them growth 3 years after seedinling establishment in a tree experiment in Cedar Creek, the Forests and Biodiversity experiment, aka FAB.

Set up your data and your working directory

Set up a working directory and put the two data files in that directory. Tell R that this is the directory you will be using, and read in your data:

```
setwd("path/for/your/directory")
```

Install and load the following packages

```
library(partitionBEFsp)
library(agricolae)
```

Part 1 - Estimating Loreau's and Hector partition

First set biomass values for N species in both monocultures and mixtures

```r
#Monoculture biomasses for 50 species
M <- c(57.57, 2.33, 306.25, 172.42, 351.48, 280.15, 216.93,
     1.30, 397.73, 185.57, 19.81, 162.45, 36.23, 42.48,
     3.16, 250.12, 5.30, 58.06, 172.93, 210.50, 253.78,
     15.96, 218.62, 282.00, 342.73, 242.18, 49.39, 100.00,
     112.20, 181.50, 61.98, 428.82, 911.55, 80.60, 206.75,
     108.25, 58.45, 154.55, 114.58, 144.38, 273.98, 25.41,
     148.82, 48.27, 35.62, 168.45, 157.98, 100.47, 31.12,
     9.86)

#Polyculture biomasses for a community of 50 species
P <- c(31.82, 0.06, 6.93, 6.75, 0.00, 0.11, 0.00,
     10.95, 0.19, 0.58, 0.01, 0.52, 21.72, 16.20,
     0.00, 0.09, 3.42, 0.00, 0.02, 3.18, 8.86,
     0.03, 0.02, 0.00, 10.14, 8.93, 4.53, 0.00,
     0.00, 0.02, 8.80, 0.31, 21.47, 0.34, 14.52,
     0.15, 0.00, 17.17, 66.55, 1.65, 0.44, 0.17,
     7.11, 0.45, 5.37, 7.66, 4.37, 0.00, 120.08,
     144.61)
```

Now using the biomass mass values of our 50 species let's calculate the change in relative yield or Delta Relative Yield (DRY). DRY is calculated by comparing the observed relative yield to the expected yield or simply as DRY = P/M - 1/Q where is the number of species in the community.

```r
# calculate DRY
DRY <- calculate_DRY(M = M, P = P, Q = length(M))
```

Now we are ready to estimate the additive partition of local net biodiversity effect (NBE) into ist local complementary (CE) and selection (SE) components as proposed by Loreau and Hector (2001).

```r
#calculate classic partition for full community
NBE <- classic_partition(DRY = DRY, M = M)
```

```r
SE <- NBE$S
CE <- NBE$C
```

Part 2 - Exploring the effects of biodiversity on ecosystem functioning

Read in data from "Species richness and traits predict overyielding in stem growth in an early-successional tree diversity experiment" (Grossman et al. 2017; Ecology 98:2601-14)

```r
df <- read.csv("Data/BEF_Lesson_Data.csv", header = T)
```

```r
names(df)
```

"df" should now be a data frame with 9 columns and 140 rows. The rows are the 140 experimental plots in the FAB experiment. The columns are as follows:

```r
dim(df)
```

1. Plot = an arbitrary index for each plot
2. SR = species richness of the plot (1, 2, 5, or 12 species)

3. Comp = a categorical code that is the same for plots with the same composition. M = monoculture, B = biculture, F = five-species, and T = 12-species
4. PSV = phylogenetic species variability (Helmus et al. 2007) - a metric of phylogenetic diversity independent of species richness
5. FDis = functional dispersion (Laliberte and Legendre 2010) - a metric of functional diversity independent of species richness
6. NBE = net biodiversity effect - observed biodiversity (d_Y) minus expected biodiversity (based on monocultures (not give in this example)
7. CE = complementarity effects (Loreau and Hector 2001) CE + SE = NBE; calculated using a script from Forest Isbell - UMN–Twin Cities
8. SE = selection effects (Loreau and Hector 2001) see above
9. d_Y = delta biomass, the average change in stem biomass of a tree in a given plot (kg)

Important - Note that there is no value for NBE, CE, and SE for monocultures since these can only be calcluated for polycultures

Exercise 1

Question 1: does stem biomass yield depend on plot composition and richness?

First, set a color scheme to distinguish among composition by color and then, plot the data to see if there is a visible trend:

```
comp.cols <- c(rep("red", 12), rep("orange", 28), rep("yellow", 10), rep("green", 1))
```

```
with(df, plot(Comp, d_Y, col = comp.cols))
```

Now, use a regression model to assess whether there is a difference:

```
m1 <- lm(d_Y ~ Comp, data = df)
summary(m1)
```

```
anova(m1) # Use an ANOVA for categorical data
```

Since an ANOVA is significant, you can use a post-hoc test to gauge differences in composition:

```
m1.df <- HSD.test(m1, "Comp", group = TRUE, console = TRUE)
```

Wow, there is a lot of variability among plot compositions. But what if we summarize across this variability based on the number of species in the plot. Following the same steps as above:

```
with(df,plot(SR, d_Y)) #It's a little hard to assess the pattern graphically
```

```
m2 <- lm(d_Y ~ SR, data = df)
summary(m2) #A linear model indicates "no"
```

```
anova(m2) #ANOVA confirms this.
```

Please answer the following questions:

1. Do plots of different composition vary in yield?

2. What about plots that vary in species richness/diversity?

Question 2: does overyielding depend on plot composition and richness?

Keep in mind that instead of how much biomass a plot produces, the response variable is now that number MINUS what would be expected if each tree in the plot were growing in monoculture. So, this adjusts for the "innate" productivity of each species.

What about plots of different compositions?

```
with(df, plot(Comp, NBE, col = comp.cols))
```

```
m3 <- lm(NBE ~ Comp, data = df)
summary(m3)
```

```
anova(m3)
```

```
m3.df <- HSD.test(m3, "Comp", group = TRUE, console = TRUE)
```

Interesting!

3. Which four plots have the highest overyielding according to the post-hoc test?

Given this, **4. what do you expect you'l find when you assess the dependence of overyielding on species richness?**

```
with(df, plot(SR, NBE)) #Note: it doesn't make sense to plot NBE of monocultures
```

```
m4 <- lm(NBE ~ SR, data = df)
summary(m4)
```

```
anova(m4)
```

```
m4.df <- HSD.test(m4, "SR", group = TRUE, console = TRUE)
```

Take a moment to compare the output of model 4 to that of model 2.

5. This helps explain the importance of monocultural controls in biodiversity experiments.

Exercise 2

Question 3: How do different levels of species richness compare in terms of complementarity and selection?

The tools you use here should now feel familar: first, analyze graphically; then make a linear model and assess it with ANOVA if the ANOVA is significant, use post-hoc testing

First, complementarity effects:

```
with(df, plot(SR, CE))
```

```
m5 <- lm(CE ~ SR, data = df)
summary(m5)
```

```
anova(m5)
```

```
m5.df <- HSD.test(m5, "SR", group = TRUE, console = TRUE)
```

Then, selection effects:

```r
with(df, plot(SR, SE))
```

```r
m6 <- lm(SE ~ SR, data = df)
summary(m6)
```

```r
anova(m6)
```

```r
m6.df <- HSD.test(m6, "SR", group = TRUE, console = TRUE)
```

You can even plot CE and SE together

```r
with(df, plot(SR, CE, col = "blue"))
with(df, points(SR, SE, col = "red"))
abline(h = 0) #Just to make it easier to tell positive from negative
```

6. How do CE and SE compare to each other and NBE (overyielding)?

7. What does positive CE mean? What does negative CE mean?

8. What about positive and negative values of SE? (This can be confusing.)

Question 4: Do you find evidence of transgressive overyielding?

To ask this question, let's return to the plot from Question 1:

```r
with(df, plot(SR, d_Y, ylim = c(-0.05, 0.25)))
#and add a horizontal line:
abline(h = 0)
```

9. Are the least productive (or even average) polycultures more productive than the most productive monocultures?

(If you are still unconvinced, you could code all monocultures as "0" and all polycultures as "1" and do a t-test...)

Exercise 3

Question 5: Which dimension of biodiversity - taxonomic (species richness), phylogenetic, or functional diversity best predicts overyielding in productivity in the FAB experiment?

To address this question, we'll see how much of the variability in overyielding (NBE) is explained by each dimension. For a univariate regression model, we can just use R^2 from the linear model output to do model comparison.

```r
m4 <- lm(NBE ~ SR, data = df)
summary(m4) #This is our old friend from question 2.
```

```r
m7 <- lm(NBE ~ PSV, data = df)
summary(m7) # What about phylogenetic diversity?
```

```r
m8 <- lm(NBE ~ FDis, data = df)
summary(m8) # Or functional diversity?
```

So, if you had to choose one, **10. which dimension of diversity would you say best predicts overyielding in stem growth?**

11. What do you make of the differences in R^2 values for each dimension?

Optional: You can also do this analysis with CE or SE as the dependent variable.

References

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Isbell, F., Cowles, J., Dee, L. E., Loreau, M., Reich, P. B., Gonzalez, A., ... Schmid, B. (2018). Quantifying effects of biodiversity on ecosystem functioning across times and places. Ecology Letters, 21(6), 763–778. doi:10.1111/ele.12928

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