Lab 3. Quantifying Biodiversity

Smit, A. J.
University of the Western Cape

2021-01-01

Table of contents

> ℹ **BCB743**
>
> **This material must be reviewed by BCB743 students in Week 1 of Quantitative Ecology.**

> 💡 **This Lab Accompanies the Following Lecture**
>
> - Lecture 4: Biodiversity Concepts

> **💡 Data For This Lab**
>
> The seaweed (Smit et al. 2017) and toy data are at the links below:
>
> - The seaweed species data – `SeaweedSpp.csv`
> - The seaweed environmental data – `SeaweedEnv.csv`
> - The seaweed coastal sections – `SeaweedSites.csv`
> - The fictitious light data `light_levels.csv`

Biodiversity *The variability among living organisms from all sources including,* inter alia, *terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.*

— International Union for the Conservation of Nature (IUCN), Convention on Biological Diversity

The IUCN definition considers a diversity of diversity concepts. This module looks at diversity only at the species level (species diversity). However, we can also approach macro-ecological problems from phylogenetic and functional (and other) diversity concepts of view. Functional and phylogenetic diversity ideas will be introduced in the BDC743 module Quantitative Ecology.

1 Preparation

1.1 The South African Seaweed Data

In these examples, we will use the seaweed data of Smit et al. (2017). Please make sure that you read this paper. An additional file describing the background to the data is available here (Figure 1).
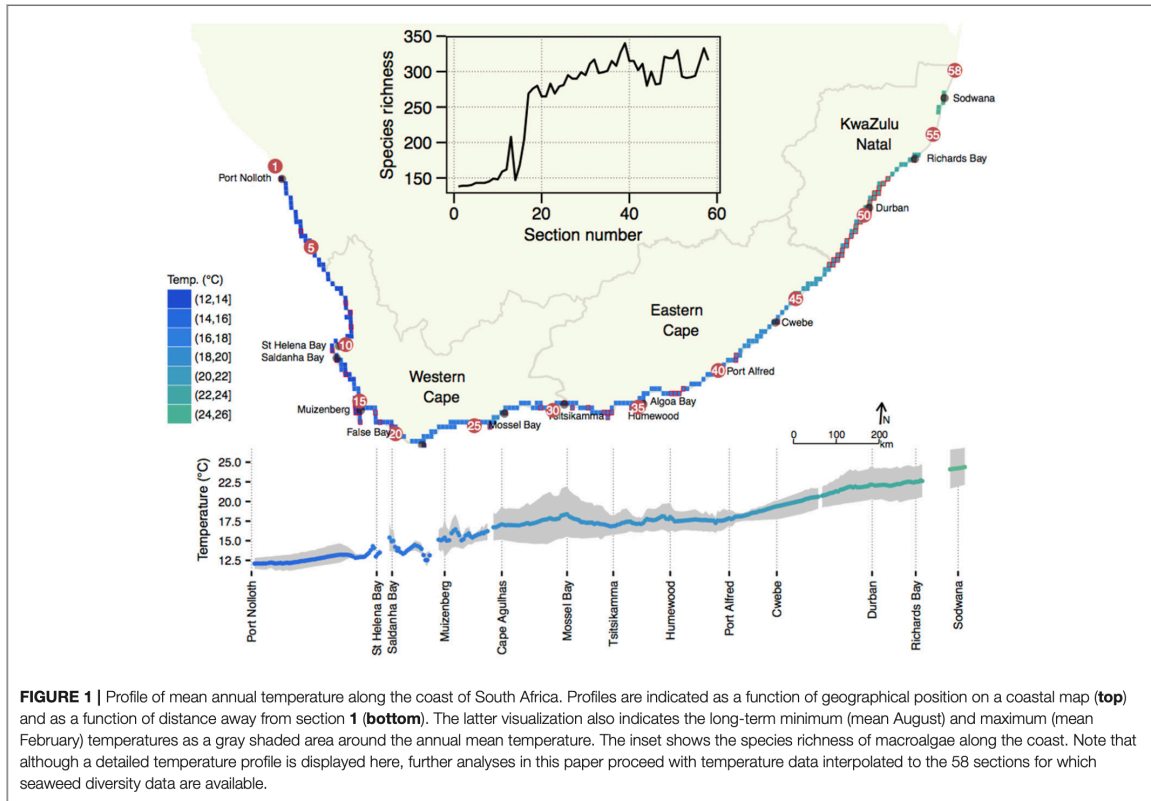
FIGURE 1 | Profile of mean annual temperature along the coast of South Africa. Profiles are indicated as a function of geographical position on a coastal map (**top**) and as a function of distance away from section **1** (**bottom**). The latter visualization also indicates the long-term minimum (mean August) and maximum (mean February) temperatures as a gray shaded area around the annual mean temperature. The inset shows the species richness of macroalgae along the coast. Note that although a detailed temperature profile is displayed here, further analyses in this paper proceed with temperature data interpolated to the 58 sections for which seaweed diversity data are available.

Figure 1: The coastal sections and associated seawater temperature profile associated with the study by Smit et al. (2017).

One of the datasets, Y (in the file `SeaweedSpp.csv`), comprises updated distribution records of 847 macroalgal species within each of 58×50 km-long sections of the South African coast (Bolton and Stegenga 2002). The dataset captures *ca.* 90% of the known seaweed flora of South Africa, but excludes some very small and/or very rare species for which data are insufficient. The data are from verifiable literature sources and John Bolton and Rob Anderson's collections, assembled from information collected by teams of phycologists over three decades (Bolton 1986, Stegenga et al. 1997, Bolton and Stegenga 2002, De Clerck et al. 2005). Another file, E (in `env.csv`), is a dataset of *in situ* coastal seawater temperatures derived from daily measurements over 40 years (Smit et al. 2013).

1.2 Setting Up the Analysis Environment

We will use **R**, so first, we must find, install and load various packages. Some packages will be available on CRAN and can be accessed and installed the usual way, but you will need to download others from R Forge.

```r
library(tidyverse)
library(vegan)
library(betapart)
```

1.3 A Look at the Data

Let's load the data and see how it is structured:

```r
spp <- read.csv(here::here("data", "seaweed", "SeaweedSpp.csv"))
spp <- dplyr::select(spp, -1)

# Lets look at the data:
dim(spp)
```

```
[1]  58 847
```

We see that our dataset has 58 rows and 847 columns. What is in the columns and rows? Start with the first five rows and five columns:

```r
spp[1:5, 1:5]
```

```
  ACECAL ACEMOE ACRVIR AROSP1 ANAWRI
1      0      0      0      0      0
2      0      0      0      0      0
3      0      0      0      0      0
4      0      0      0      0      0
5      0      0      0      0      0
```

Now the last five rows and five columns:

```r
spp[(nrow(spp) - 5):nrow(spp), (ncol(spp) - 5):ncol(spp)]
```

```
   WOMKWA WOMPAC WRAARG WRAPUR WURMIN ZONSEM
53      0      0      1      0      0      0
54      0      0      1      0      0      0
55      0      0      1      0      0      0
56      0      1      1      0      1      0
57      1      0      1      0      1      0
58      0      0      1      0      1      0
```

So, each row corresponds to a site (i.e. each of the coastal sections), and each column contains a species. We arrange the species alphabetically and use a six-letter code to identify them.

2 Species Data

When ecologists talk about species diversity, they typically consider the characteristics of biological communities in a specific habitat, ecological community, or ecosystem. Species diversity considers three essential concepts about how species are distributed in space: their **richness**, **abundance**, and **evenness**. We can express each of these as biodiversity metrics that allow us to compare communities in space and time.

When ecologists talk about 'biodiversity', they might not necessarily be interested in *all* the plants and animals and things that are neither plant nor animal that occur at a particular place. Some ecologists are interested in ants and moths. Others might find fish more insightful. Some even like marine mammals! I prefer seaweed. The analysis of biodiversity data might often be constrained to some higher-level taxon, such as all angiosperms in a landscape, reptiles, etc. (but we sample all species in the higher-level taxon). Some ecological questions benefit from comparisons of diversity assessments among selected taxa (avifauna vs small mammals, for example), as this focus might address some particular ecological hypothesis. The bird vs small mammal comparison might reveal how barriers such as streams and rivers structure biodiversity patterns. In our examples, we will use such focused datasets.

Here we look at the various measures of biodiversity, viz. α-, γ- and β-diversity. David Zelený, in his Analysis of community data in R, provides deeper analysis and compulsory reading.

3 Three Measures of Biodiversity: α-, γ-, β-Diversity

Whittaker (1972) coined three measures of biodiversity, and the concepts were 'modernised' by Jurasinski et al. (2009). The concepts represent the measurement of biodiversity *across different spatial scales*. α- and γ-diversity express the total number of species in an area. The first, α-diversity, represents the number of species at the small (local) scale, such as, for example, within a sampling unit like a quadrat, transect, plot, or trawl. Alternatively, maybe the research question represents the local scale by several sampling units nesting within a small patch of landscape and defines the mean species richness within this patch as local. Multiples (sampling units or patches) are nested within a larger region (or ecosystem) and serve as replicates. The complete number of species across all of these replicates indicates the diversity at a larger scale—this is called γ-diversity. β-diversity refers to the change in species composition among samples (sites).

By now, you will have received a brief Introduction to R, and we can proceed with looking at some of the measures of biodiversity. We will start by using data on the seaweeds of South Africa to demonstrate some ideas around diversity measures. The **vegan**[1] (for *vegetation analysis*) package (Oksanen et al. 2022) offers various functions to calculate diversity indices. I will demonstrate some of these functions below.

3.1 Alpha-Diversity

We can represent α-diversity in three ways:

1. as *species richness*, S;
2. as a *univariate diversity index*, such as the α parameter of Fisher's log-series, Shannon diversity, H', Simpson's diversity, λ; or
3. Species *evenness*, e.g. Pielou's evenness, J.

We will work through each in turn.

3.1.1 Species Richness, S

First, is species richness, which we denote by the symbol S. This is the simplest measure of α-diversity, counting the number of species (or another taxonomic level) present in a given community or sample. It doesn't consider the abundance of species.

In the seaweed biodiversity data, I count the number of species within each of the sections. This is because we view each coastal section as the local scale (the smallest unit of sampling).

The preferred option for calculating species richness is the `specnumber()` function in **vegan**:

```
specnumber(spp, MARGIN = 1)
```

Line 1

   The `MARGIN = 1` argument tells R to calculate the number of species within each row (site).

```
 [1] 138 139 139 140 143 143 143 145 149 148 159 162 208 147 168 204
269 276 280
[20] 265 265 283 269 279 281 295 290 290 299 295 311 317 298 299 301
315 308 327
[39] 340 315 315 302 311 280 300 282 283 321 319 319 330 293 291 292
294 313 333
[58] 316
```

The data output is easier to understand if we display it as a `tibble()`:

---

[1] I am by no means an advocate for veganism.

```
spp_richness <- tibble(section = 1:58,
  richness = specnumber(spp, MARGIN = 1))
head(spp_richness)
```

```
# A tibble: 6 × 2
  section richness
    <int>    <int>
1       1      138
2       2      139
3       3      139
4       4      140
5       5      143
6       6      143
```

Now we make a plot seen in Figure 2:

```
ggplot(data = spp_richness, (aes(x = 1:58, y = richness))) +
  geom_line(size = 1.2, colour = "indianred") +
  xlab("Coastal section, west to east") +
  ylab("Species richness") +
  theme_linedraw()
```
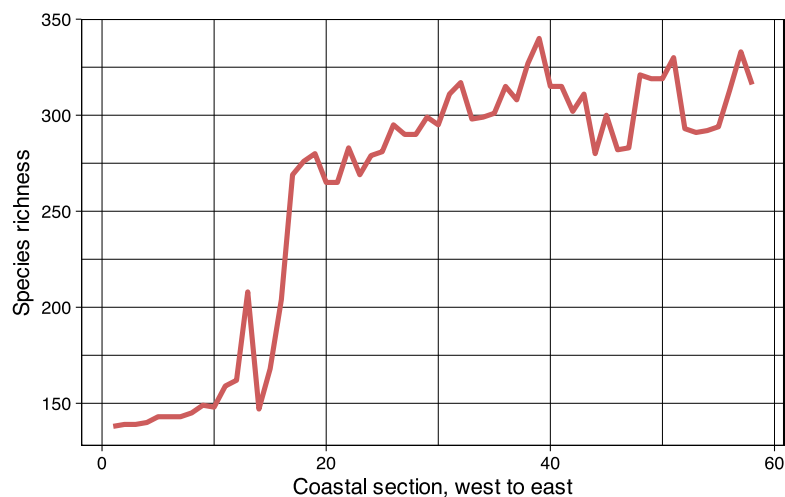

Figure 2: The seaweed species richness, S, within each of the coastal sections along the shore of South Africa.

In other instances, it makes more sense to calculate the mean species richness of all the sampling units (e.g. quadrats) taken inside the ecosystem of interest. How you calculate and

present species richness depend on your research question and so you will have to decide based on your data and study.

In the seaweed study, the mean ± SD species richness across all of the 58 coastal sections is:

```
round(mean(spp_richness$richness), 2)
```

```
[1] 259.24
```

```
round(sd(spp_richness$richness), 2)
```

```
[1] 68.03
```

3.1.2 Univariate Diversity Indices

The second way we can express α-diversity is to use one of the univariate diversity indices. The choice of which index to use should be informed by the extent to which one wants to emphasise richness or evenness. Species richness, S, does not consider evenness as it is all about richness (obviously). Simpson's λ emphasises evenness a lot more. Shannon's H' is somewhere in the middle.

Shannon's H' is sometimes called Shannon's diversity, the Shannon-Wiener index, the Shannon-Weaver index, or the Shannon entropy. This is a more nuanced measure that considers both species richness and evenness (how evenly individuals are distributed across different species).

It is calculated as:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

where p_i is the proportion of individuals belonging to the i-th species, and S is the species richness.

Simpson's λ, or simply the Simpson index, is a measure that represents the probability that two individuals randomly selected from a sample will belong to the same species. It is calculated as:

$$\lambda = \sum_{i=1}^{S} p_i^2$$

where S is the species richness and p_i is the relative abundance of the ith species.

Fisher's α estimates the α parameter of Fisher's logarithmic series (see functions `fisher.alpha()` and `fisherfit()`). The estimation is possible only for actual counts (i.e. integers) of individuals, so it will not work for per cent cover, biomass, and other measures that real numbers can express. It's especially useful for comparing the diversity of samples with different total abundances. We will get to this function later under Fisher's logarithmic series.

Except for Fisher's-α, we cannot calculate these for the seaweed data, because, in order to do so, we require abundance data—the seaweed data are presence-absence only. Let us load a fictitious dataset of the diversity of three different communities of plants, with each community corresponding to a different light environment (dim, mid, and high light):

```
light <- read.csv(here::here("data", "light_levels.csv"))
light
```

```
       Site    A    B    C    D    E    F
1   low_light 0.75 0.62 0.24 0.33 0.21 0.14
2   mid_light 0.38 0.15 0.52 0.57 0.28 0.29
3 high_light 0.08 0.15 0.18 0.52 0.54 0.56
```

We can see above that instead of having data with 1s and 0s for presence-absence, here we have some values that indicate the relative number of individuals belonging to each of the species in the three light environments. We calculate species richness (as before), and also the Shannon and Simpson indices using **vegan**'s `diversity()` function:

```
light_div <- tibble(
  site = c("low_light", "mid_light", "high_light"),
  richness = specnumber(light[, 2:7], MARGIN = 1),
  shannon = round(diversity(light[, 2:7], MARGIN = 1, index =
"shannon"), 2),
  simpson = round(diversity(light[, 2:7], MARGIN = 1, index =
"simpson"), 2)
)
light_div
```

```
# A tibble: 3 × 4
  site       richness shannon simpson
  <chr>         <int>   <dbl>   <dbl>
1 low_light         6    1.62    0.78
2 mid_light         6    1.71    0.81
3 high_light        6    1.59    0.77
```

Evenness refers to the shape of a species abundance distribution, which suggests the relative abundance of different species.

One index for evenness is Pielou's evenness, J:

$$J = \frac{H'}{log(S)}$$

where H' is Shannon's diversity index, and S the number of species (i.e. S).

To calculate Pielou's evenness index for the `light` data, we can do this:

```
H <- diversity(light[, 2:7], MARGIN = 1, index = "shannon")

J <- H/log(specnumber(light[, 2:7]))
round(J, 2)
```

```
[1] 0.91 0.95 0.89
```

Berger-Parker Index indicates the proportion of the community that the most abundant species represents. It is given by the formula:

$$d = \frac{N_{max}}{N}$$

where N_{max} is the number of individuals of the most common species and N is the total number of individuals in the sample.

Chao1 and **ACE** are estimators often used to predict the total species richness in a community based on the number of rare species observed in samples.

3.2 Gamma-Diversity

Returning to the seaweed data, Y, let us now look at γ-diversity—this would be the total number of species along the South African coastline in all 58 coastal sections. Since each column represents one species, and the dataset contains data collected at each of the 58 sites (the number of rows), we can do:

```
ncol(spp) # <1>`
```

```
[1] 847
```

1. The number of columns gives the total number of species in this example.

We can also use the `specnumber()` function to calculate γ-diversity by applying it to columns where the `sum > 0`:

```
richness_pooled <- specnumber(colSums(spp > 0))
richness_pooled
```

```
[1] 846
```

> **!** Lab 3
>
> (To be reviewed by BCB743 student but not for marks)
>
> 1. Why is there a difference between the two?
> 2. Which is correct?

Think before you calculate γ-diversity for your own data as it might not be as simple as here!

3.3 Beta-Diversity

3.3.1 Whittaker's β-Diversity

The first measure of β-diversity comes from Whittaker (1960) and is called *true β-diversity*. In this instance, divide the γ-diversity for the region by the α-diversity for a specific coastal section. We can calculate it all at once for the whole dataset and make a graph (Figure 3):

```
true_beta <- data.frame(
  beta = specnumber(spp, MARGIN = 1) / ncol(spp),
  section_no = c(1:58)
)
# true_beta
ggplot(data = true_beta, (aes(x = section_no, y = beta))) +
  geom_line(size = 1.2, colour = "indianred") +
  xlab("Coastal section, west to east") +
  ylab("True beta-diversity") +
  theme_linedraw()
```
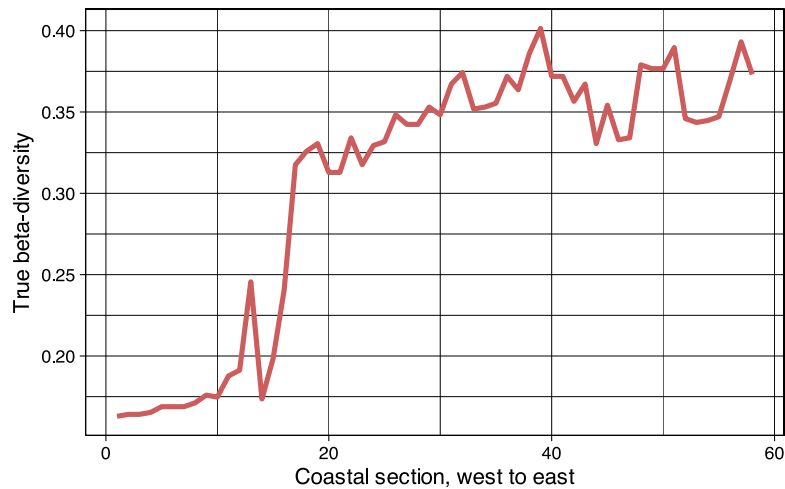
Figure 3: Whittaker's true β-diversity shown in the seaweed data.

The second measure of β-diversity is *absolute species turnover*, and to calculate this, we subtract α-diversity for each section from the region's γ-diversity (Figure 4):

```r
abs_beta <- data.frame(
  beta = ncol(spp) - specnumber(spp, MARGIN = 1),
  section_no = c(1:58)
)
# abs_beta
ggplot(data = abs_beta, (aes(x = section_no, y = beta))) +
  geom_line(size = 1.2, colour = "indianred") +
  xlab("Coastal section, west to east") +
  ylab("Absolute beta-diversity") +
  theme_linedraw()
```
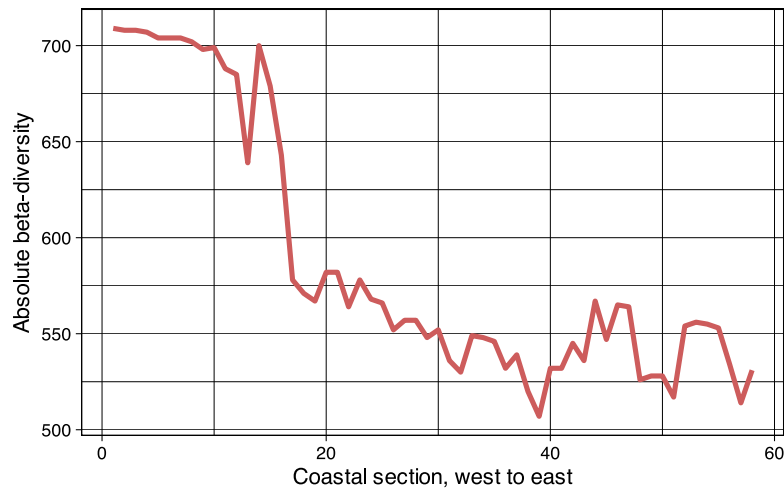
Figure 4: Whittaker's absolute species turnover shown in action in the seaweed data.

3.3.2 Contemporary Definitions β-Diversity

Contemporary definitions of β-diversity are anchored in pairwise *dissimilarity indices* such as Bray–Curtis, Jaccard, or Sørensen dissimilarities—see Koleff et al. (2003) for a broader catalogue, and consult `?vegdist` for implementation details.

3.3.2.1 Dissimilarity indices

Dissimilarity indices constitute a subset of diversity measures that rely on pairwise comparisons between sampling units, habitats, or ecosystems.

The outcome of such comparisons is a *pairwise matrix* of species dissimilarities, directly analogous to the correlation and Euclidean distance matrices introduced in Lab 1. In Lab 2b you learned how to compute these ecological distances in **R**. Unlike univariate diversity indices, these measures are multivariate, designed to quantify differences between sites, plots, or regions rather than summarising properties of a single community.

Different indices are used depending on the data structure: Bray–Curtis and Jaccard for abundance data, and Sørensen for presence–absence data. Because the seaweed dataset is presence–absence, Sørensen is the appropriate choice. Regardless of whether the matrix derives from abundance or presence–absence data, the interpretation is consistent: values range from 0 (two sites share all species) to 1 (no species in common). By construction, the diagonal is always 0, since any site is identical to itself.

For the seaweed dataset of 58 sites, the pairwise comparison yields

$$(58 \times (58 - 1))/2 = 1653$$

13

unique values, each falling between 0 and 1. These entries populate a symmetric square matrix whose structure is both intuitive and mathematically consistent: the ecological distance between sites is expressed in a form readily amenable to further multivariate analysis.

The first step begins with the species table, Y. Using presence–absence data, we compute the Sørensen dissimilarity index, $\beta_{\text{sør}}$, which quantifies the dissimilarity between all pairs of coastal sections. This measure is derived from three quantities: a, the number of species shared by both sites; and b and c, the numbers of species unique to each site. Formally,

$$\beta_{\text{sør}} = \frac{2a}{2a + b + c}.$$

Here, a denotes the species common to both sites, while b and c capture the exclusive species of each. The index ranges from 0 to 1: a value of 0 indicates identical species composition (complete overlap), whereas a value of 1 indicates complete dissimilarity (no overlap).

In practice, the vegan function vegdist() provides access to a range of dissimilarity indices, including Sørensen, which we apply to the species table to generate the full pairwise matrix.

```
sor <- vegdist(spp, binary = TRUE) # makes the lower triangle matrix
sor_df <- round(as.matrix(sor), 4)
dim(sor_df)
```

```
[1] 58 58
```

```
sor_df[1:10, 1:10] # display only the first 10 rows and columns
```

```
        1      2      3      4      5      6      7      8      9
10
1  0.0000 0.0036 0.0036 0.0072 0.0249 0.0391 0.0391 0.0459 0.0592
0.0629
2  0.0036 0.0000 0.0000 0.0036 0.0213 0.0355 0.0355 0.0423 0.0556
0.0592
3  0.0036 0.0000 0.0000 0.0036 0.0213 0.0355 0.0355 0.0423 0.0556
0.0592
4  0.0072 0.0036 0.0036 0.0000 0.0177 0.0318 0.0318 0.0386 0.0519
0.0556
5  0.0249 0.0213 0.0213 0.0177 0.0000 0.0140 0.0140 0.0208 0.0342
0.0378
6  0.0391 0.0355 0.0355 0.0318 0.0140 0.0000 0.0000 0.0069 0.0205
0.0241
7  0.0391 0.0355 0.0355 0.0318 0.0140 0.0000 0.0000 0.0069 0.0205
```

```
0.0241
8   0.0459 0.0423 0.0423 0.0386 0.0208 0.0069 0.0069 0.0000 0.0136
0.0171
9   0.0592 0.0556 0.0556 0.0519 0.0342 0.0205 0.0205 0.0136 0.0000
0.0034
10 0.0629 0.0592 0.0592 0.0556 0.0378 0.0241 0.0241 0.0171 0.0034
0.0000
```

What we see above is a square dissimilarity matrix. The most important characteristics of the matrix are:

i. whereas the raw species data, Y, is rectangular (number rows ≠ number columns), the dissimilarity matrix is square (number rows = number columns);
ii. the number of rows/columns is equal to the number of sites (58 in this case);
iii. the diagonal is filled with 0;
iv. the matrix is symmetrical—it is comprised of symetrical upper and lower triangles.

To continue using the dissimilarity matrix, it helps if we convert it to `data.frame`. This makes the matrix more amenable to a host of subsequent manipulations, including using it for plotting:

```
sor_df <- data.frame(round(as.matrix(sor), 4))
```

> **!** Lab 3
>
> (To be reviewed by BCB743 student but not for marks)
>
> These questions concern matrices produced from species data using any of the indices available in `vegdist()`:
>
> 3. Why is the matrix square, and what determines the number of rows/columns?
> 4. What is the meaning of the diagonal?
> 5. What is the meaning of the non-diagonal elements?
> 6. Referring to the seaweed species data specifically, take the data in row 1 or column 1 and create a line graph showing these values as a function of the section number.
> 7. Provide a mechanistic (ecological) explanation for why this figure takes the shape that it does. Which community assembly process does this hint at?

There are different interpretations linked to β-diversity, each telling us something different about community formation processes.

3.3.2.2 Species turnover and nestedness-resultant β-diversity

There are two principal forms of β-diversity: species turnover and nestedness-resultant β-diversity. Turnover reflects species replacement between sites, whereas nestedness-resultant β-diversity reflects ordered species loss or gain. The Sørensen index, $\beta_{\mathrm{sør}}$, can be partitioned into these two components.

To calculate them, we rely on the **betapart** package (Baselga et al. 2022), which implements the framework introduced by Baselga (2010). The decomposition separates $\beta_{\mathrm{sør}}$ into β_{sim} (turnover) and β_{sne} (nestedness-resultant) components, using the functions `betapart.core()` and `betapart.pair()`. The resulting matrices, $Y1$ and $Y2$, contain these partitioned dissimilarities.

Once obtained, these matrices can serve as the basis for subsequent multivariate analyses—for instance, principal components analysis (PCA) or related ordination techniques applied to Y to identify dominant community patterns. We will pursue such analyses in BCB743.

```
# Decompose total Sørensen dissimilarity into turnover and nestedness-
resultant
# components:
Y.core <- betapart.core(spp)
Y.pair <- beta.pair(Y.core, index.family = "sor")

# Let Y1 be the turnover component (beta-sim):
Y1 <- data.frame(round(as.matrix(Y.pair$beta.sim), 3))

# Let Y2 be the nestedness-resultant component (beta-sne):
Y2 <- data.frame(round(as.matrix(Y.pair$beta.sne), 3))
```

A portion of the turnover component matrix:

```
Y1[1:10, 1:10]
```

```
      X1    X2    X3    X4    X5    X6    X7    X8    X9   X10
1  0.000 0.000 0.000 0.000 0.007 0.022 0.022 0.022 0.022 0.029
2  0.000 0.000 0.000 0.000 0.007 0.022 0.022 0.022 0.022 0.029
3  0.000 0.000 0.000 0.000 0.007 0.022 0.022 0.022 0.022 0.029
4  0.000 0.000 0.000 0.000 0.007 0.021 0.021 0.021 0.021 0.029
5  0.007 0.007 0.007 0.007 0.000 0.014 0.014 0.014 0.014 0.021
6  0.022 0.022 0.022 0.021 0.014 0.000 0.000 0.000 0.000 0.007
7  0.022 0.022 0.022 0.021 0.014 0.000 0.000 0.000 0.000 0.007
8  0.022 0.022 0.022 0.021 0.014 0.000 0.000 0.000 0.000 0.007
```

```
9  0.022 0.022 0.022 0.021 0.014 0.000 0.000 0.000 0.000 0.000
10 0.029 0.029 0.029 0.029 0.021 0.007 0.007 0.007 0.000 0.000
```

A portion of the nestedness-resultant matrix:

```
Y2[1:10, 1:10]
```

```
      X1    X2    X3    X4    X5    X6    X7    X8    X9   X10
1  0.000 0.004 0.004 0.007 0.018 0.017 0.017 0.024 0.037 0.034
2  0.004 0.000 0.000 0.004 0.014 0.014 0.014 0.021 0.034 0.030
3  0.004 0.000 0.000 0.004 0.014 0.014 0.014 0.021 0.034 0.030
4  0.007 0.004 0.004 0.000 0.011 0.010 0.010 0.017 0.030 0.027
5  0.018 0.014 0.014 0.011 0.000 0.000 0.000 0.007 0.020 0.017
6  0.017 0.014 0.014 0.010 0.000 0.000 0.000 0.007 0.021 0.017
7  0.017 0.014 0.014 0.010 0.000 0.000 0.000 0.007 0.021 0.017
8  0.024 0.021 0.021 0.017 0.007 0.007 0.007 0.000 0.014 0.010
9  0.037 0.034 0.034 0.030 0.020 0.021 0.021 0.014 0.000 0.003
10 0.034 0.030 0.030 0.027 0.017 0.017 0.017 0.010 0.003 0.000
```

A portion of the nestedness-resultant matrix reformatted as a `tibble()`[2], which is a modern take on a dataframe.:

```
Y2_tib <- as_tibble(Y2)
head(Y2_tib)
```

```
# A tibble: 6 × 58
     X1    X2    X3    X4    X5    X6    X7    X8    X9   X10   X11
X12   X13
  <dbl> <dbl> <dbl> <dbl> <dbl> <dbl> <dbl> <dbl> <dbl> <dbl> <dbl>
<dbl> <dbl>
1 0     0.004 0.004 0.007 0.018 0.017 0.017 0.024 0.037 0.034 0.069
0.078 0.196
2 0.004 0     0     0.004 0.014 0.014 0.014 0.021 0.034 0.03  0.065
0.074 0.193
3 0.004 0     0     0.004 0.014 0.014 0.014 0.021 0.034 0.03  0.065
0.074 0.193
4 0.007 0.004 0.004 0     0.011 0.01  0.01  0.017 0.03  0.027 0.062
0.071 0.19
5 0.018 0.014 0.014 0.011 0     0     0     0.007 0.02  0.017 0.052
0.061 0.181
```

---

[2]Note that the rows are no longer numbered in the tibble view, but it can easily be recreated by `seq(1:58)`.

```
6 0.017 0.014 0.014 0.01  0     0     0     0.007 0.021 0.017 0.053
0.062 0.184
# i 45 more variables: X14 <dbl>, X15 <dbl>, X16 <dbl>, X17 <dbl>, X18
<dbl>,
#   X19 <dbl>, X20 <dbl>, X21 <dbl>, X22 <dbl>, X23 <dbl>, X24 <dbl>,
#   X25 <dbl>, X26 <dbl>, X27 <dbl>, X28 <dbl>, X29 <dbl>, X30 <dbl>,
#   X31 <dbl>, X32 <dbl>, X33 <dbl>, X34 <dbl>, X35 <dbl>, X36 <dbl>,
#   X37 <dbl>, X38 <dbl>, X39 <dbl>, X40 <dbl>, X41 <dbl>, X42 <dbl>,
#   X43 <dbl>, X44 <dbl>, X45 <dbl>, X46 <dbl>, X47 <dbl>, X48 <dbl>,
#   X49 <dbl>, X50 <dbl>, X51 <dbl>, X52 <dbl>, X53 <dbl>, X54 <dbl>, …
```

```
# this is functionally eqivalent to:
Y2_df <- round(as.matrix(Y2), 4)
head(Y2_df)[, 1:13]
```

```
     X1    X2    X3    X4    X5    X6    X7    X8    X9   X10   X11
X12   X13
1 0.000 0.004 0.004 0.007 0.018 0.017 0.017 0.024 0.037 0.034 0.069
0.078 0.196
2 0.004 0.000 0.000 0.004 0.014 0.014 0.014 0.021 0.034 0.030 0.065
0.074 0.193
3 0.004 0.000 0.000 0.004 0.014 0.014 0.014 0.021 0.034 0.030 0.065
0.074 0.193
4 0.007 0.004 0.004 0.000 0.011 0.010 0.010 0.017 0.030 0.027 0.062
0.071 0.190
5 0.018 0.014 0.014 0.011 0.000 0.000 0.000 0.007 0.020 0.017 0.052
0.061 0.181
6 0.017 0.014 0.014 0.010 0.000 0.000 0.000 0.007 0.021 0.017 0.053
0.062 0.184
```

> **!** Lab 3 (continue)
>
> (To be reviewed by BCB743 student but not for marks)
>
> 8. Plot species turnover as a function of Section number, and provide a mechanistic explanation for the pattern observed.
> 9. Based on an assessment of literature on the topic, provide a discussion of nestedness-resultant β-diversity. Use either a marine or terrestrial example to explain this mode of structuring biodiversity (i.e. assembly of species into a community).

> **! Submission Instructions**
>
> The Lab 3 assignment is due at **08:00 on Monday 18 August 2025**.
>
> Provide a **neat and thoroughly annotated** R file which can recreate all the graphs and all calculations. Written answers must be typed in the same file as comments.
>
> Please label the R file as follows:
>
> - `BDC334_<first_name>_<last_name>_Lab_3.R`
>
> (the < and > must be omitted as they are used in the example as field indicators only).
>
> Submit your appropriately named R documents on iKamva when ready.
>
> Failing to follow these instructions carefully, precisely, and thoroughly will cause you to lose marks, which could cause a significant drop in your score as formatting counts for 15% of the final mark (out of 100%).

Bibliography

Baselga A, Orme D, Villeger S, De Bortoli J, Leprieur F, Logez M (2022) betapart: Partitioning Beta Diversity into Turnover and Nestedness Components.

Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19:134–143.

Bolton J (1986) Marine phytogeography of the Benguela upwelling region on the west coast of southern Africa: a temperature dependent approach.

Bolton J, Stegenga H (2002) Seaweed species diversity in South Africa. South African Journal of Marine Science 24:9–18.

De Clerck O, Bolton J, Anderson R, Coppejans E, Bolton J, Anderson R (2005) Guide to the seaweeds of KwaZulu-Natal.

Jurasinski G, Retzer V, Beierkuhnlein C (2009) Inventory, differentiation, and proportional diversity: a consistent terminology for quantifying species diversity. Oecologia 159:15–26.

Koleff P, Gaston KJ, Lennon JJ (2003) Measuring beta diversity for presence–absence data. Journal of Animal Ecology 72:367–382.

Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara R, Solymos P, Stevens MHH, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista HBA, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill MO, Lahti L, McGlinn D, Ouellette M-H, Ribeiro

Cunha E, Smith T, Stier A, Ter Braak CJ, Weedon J (2022) vegan: Community Ecology Package.

Smit AJ, Bolton JJ, Anderson RJ (2017) Seaweeds in two oceans: beta-diversity. Frontiers in Marine Science 4:404.

Smit AJ, Roberts M, Anderson RJ, Dufois F, Dudley SF, Bornman TG, Olbers J, Bolton JJ (2013) A coastal seawater temperature dataset for biogeographical studies: large biases between in situ and remotely-sensed data sets around the coast of South Africa. PLoS One 8:e81944.

Stegenga H, Bolton JJ, Anderson RJ (1997) Seaweeds of the South African west coast.

Whittaker RH (1972) Evolution and measurement of species diversity. Taxon 21:213–251.

Whittaker RH (1960) Vegetation of the Siskiyou mountains, Oregon and California. Ecological Monographs 30:279–338.