

ESA Workshop

8 August, 2016

In this portion of the workshop, we will demonstrate the approaches we will use to analyze the LTER metacommunity datasets. Today, we will walk through the following analyses:

- 1) Diversity Partitioning [Jost, 2007]
- 2) Variation Partitioning [Borcard et al., 1992, Legendre et al., 2005]
- 3) Elements of Metacommunity Structure [Leibold and Mikkelsen, 2002, Presley et al., 2010]

Initial Setup

First, we will setup RStudio so it knows where to find our data files. We also load the R packages required to conduct the analyses. The loop below will try to load the packages and install them if needed.

```
# Set working environment
rm(list = ls())
setwd("~/GitHub/ltermetacommunities/ESA_2016/")

# Check for and install required packages
for (package in c('dplyr', 'tidyr', 'vegetarian', 'vegan', 'metacom')) {
  if (!require(package, character.only=T, quietly=T)) {
    install.packages(package)
    library(package, character.only=T)
  }
}

##
## Attaching package: 'dplyr'

## The following objects are masked from 'package:stats':
##
##   filter, lag

## The following objects are masked from 'package:base':
##
##   intersect, setdiff, setequal, union

## This is vegan 2.4-0
```

Dataset: NWT Plant Communities

```
# Read in NWT plant community data and site coordinates
nwt.xy <- read.csv("NWT_coordinates.csv")
nwt.comm.long <- read.csv("NWT_plantcomp.csv")[,c(2,4,5,6)]
dim(nwt.comm.long) # note long format

## [1] 19910      4

# Convert to wide format
nwt.comm.wide <- tidyr::spread(nwt.comm.long,
                               USDA_code, abund,
```

```

                                fill = 0)
dim(nwt.comm.wide) # note wide format

```

```
## [1] 968 111
```

Metacommunity analyses at a single time point:

Here, we will demonstrate the analyses at one time point. Here, we'll look at the NWT community during the year 2006.

```

# First, we'll select an individual year
nwt.2006 <- filter(nwt.comm.wide, year == 2006)
head(nwt.2006)

```

```

##   plot year 2COMP 2FORB 2GENT 2GRAM 2LICHN 2MOSS 2UNK ALGE ANME2 ANRO2
## 1    1 2006     0     0     0     0     32     0     0     0     0     0
## 2    2 2006     0     0     0     0      0     3     0     0     0     0
## 3    3 2006     0     0     0     0      0     0     0     0     0     0
## 4    4 2006     0     0     0     0      1     1     0     0     0     0
## 5    5 2006     0     0     0     0      0     0     0     0     0     0
## 6    6 2006     0     0     0     0      0     0     0     0     0     0
##   ANSE4 ARFEF3 ARPA18 ARSC CAAL6 CACA12 CACA13 CAEL3 CAHA6 CAHEE CALA10
## 1     0      0      0     0      0      0      0      0      0      0      0
## 2     0      0      0     1      0      0      0      0      0      0      0
## 3     0      0      0     0      0      0      0      0      0      0      0
## 4     0      0      0    22      0      0      0      0      0      0      0
## 5     0      0      0     0      0      0      0      0      0      0      0
## 6     0      0      0     9      0      0      0      0      0      0      0
##   CALE4 CAMPA CANI2 CAOC4 CAPE12 CAPH2 CAPU CAPY3 CAREX CARO2 CARUD CASCS2
## 1     0      0      0      0      0      0      0      0      0      0      0      0
## 2     0      0      0      0      0      0      0      0      0      0      0      0
## 3     0      0      0      0      0      0      0      0      0      0      0      12
## 4     1      0      0      7      0      0      0      0      0      0      0      0
## 5     0      0      0      0      0      0      0      0      0      0      0      0
## 6     0      0      0      0      0      0      0      0      0      0      0      0
##   CAUN2 CEARS2 CERAS CHANA2 CHJA DECE DRABA DRAU DRBRC DRST4 ELTRT EPAN4
## 1     0      0      0      0      0      0      0      0      0      0      0      0
## 2     0      0      0      0      0      45      0      0      0      0      0      0
## 3     0      0      0      0      0      0      0      0      0      0      0      0
## 4     0      0      0      0      2     23      0      0      0      0      0      0
## 5     0      0      0      0      0      45      0      0      0      0      0      0
## 6     0      0      0      0      0     14      0      0      0      0      0      0
##   ERCA14 ERIGE2 ERME2 ERNA ERPI6 ERSI3 FEBR GEAL2 GEAMA GEROT HEMO3 JUDR
## 1     0      0      0      0      0      0      0      0      0      0      0      0
## 2     0      0      0      0      0      0      8      0      0      49      0      0
## 3     0      0      0      0      0      0      0      0      0      99      0      0
## 4     0      0      0      0      0      5      9      0      0      29      0      0
## 5     0      0      0      0      0      1      0      0      0      11      0      0
## 6     0      0      0      0      0      3      0      0      0      24      0      0
##   KOMY LEPY2 LLSE LUSP4 MELA3 MEOB MIOB2 MIRU3 NOMO2 ORALA OXDI3 PACA15
## 1     0      0      0      0      0      0      0      0      0      0      0      0
## 2     0      0      0      0      0      0      0      0      0      0      0      0
## 3     0      0      0      0      5      0      0      0      0      0      0      0
## 4     0      0      0      5      0      0      3      0      0      0      0      0

```

```

## 5      0      0      0      4      0      0      4      0      0      0      0      0
## 6      0      0      0      0      0      0      2      0      0      0      0      0
##      PACR5 PAPU2 PEGR2 PHAL2 PHPU5 POA POAL2 POARG POBI6 PODI2 POGLR2 POTEN
## 1      0      0      0      0      0      0      0      0      0      0      0      0
## 2      0      0      0      0      0      0      0      1     15      0      0      0
## 3      0      0      0      0      0      0      0      0      0      1      0      0
## 4      0      0      0      0      0      0      0      0      5      0      0      0
## 5      0      0      0      0      0      0      0      0      2      0      0      0
## 6      0      0      0      0      0      0      0      0      6      0      0      0
##      POVI POVI3 PRAN PRPA RAAD RHIN11 RHRH4 SAGL SANI8 SAPE18 SAPL2 SARH2
## 1      0      0      0      0      0      0      0      0      0      0      0      0
## 2      0      0      0      0      2      0      0      0      0      0      0      0
## 3      0      0      0      0      0      0      0      0      0      0      0      0
## 4      0      0      0      0      0      0      0      0      0      0      0      0
## 5      0      0      0      0      1      0      0      0      0      0      0      0
## 6      0      0      0      0      2      0      0      0      0      0      0      0
##      SEDES SEFRB SELA SIACS2 SIPR SOMU SOSIN STELL STL02 TEACC TEGR3 TOPY
## 1      0      0      0      0      0      0      0      0      0      0      0      0
## 2      0      0      0      0      35     0      0      0      0      0      0      0
## 3      0      0      0      0      0      0      0      0      0      0      0      0
## 4      0      0      0      0      2      0      0      0      0      0      0      0
## 5      0      0      0      0      36     0      0      0      0      0      0      0
## 6      0      0      0      1     23      0      0      0      0      0      0      0
##      TRDA2 TRNA2 TRPAP TRSP2
## 1      0      0      0      0
## 2      0      0     12      0
## 3      0      0      0      0
## 4      0      0      4      0
## 5      0      0     11      0
## 6      0      0     19      6

```

```

nwt.2006 <- nwt.2006[,-c(1:2)] # remove the plot and year columns
nwt.2006 <- nwt.2006[,-which(colSums(nwt.2006) == 0)] # remove empty columns
dim(nwt.2006)

```

```
## [1] 88 71
```

Diversity Partitioning

Using the `vegetarian` package, we can partition metacommunity diversity into its local (alpha), among-site (beta) and regional (gamma) components. Additionally, we can use metrics that are biased toward rare taxa (e.g., richness, where rare and common taxa are weighted equally) or common taxa (e.g., Simpson's index).

```

# q = 0, Richness (biased toward rare species)
(nwt.2006.0.a <- vegetarian::d(nwt.2006, lev = "alpha", q = 0))

```

```
## [1] 11.5
```

```
(nwt.2006.0.b <- vegetarian::d(nwt.2006, lev = "beta", q = 0))
```

```
## [1] 6.173913
```

```
(nwt.2006.0.g <- vegetarian::d(nwt.2006, lev = "gamma", q = 0))
```

```
## [1] 71
```

```

# q = 1, Shannon
(nwt.2006.1.a <- vegetarian::d(nwt.2006, lev = "alpha", q = 1))

## [1] 5.464841

(nwt.2006.1.b <- vegetarian::d(nwt.2006, lev = "beta", q = 1))

## [1] 4.493377

(nwt.2006.1.g <- vegetarian::d(nwt.2006, lev = "gamma", q = 1))

## [1] 24.55559

# q = 2, Simpson (biased toward common species)
(nwt.2006.2.a <- vegetarian::d(nwt.2006, lev = "alpha", q = 2))

## [1] 3.440797

(nwt.2006.2.b <- vegetarian::d(nwt.2006, lev = "beta", q = 2))

## [1] 4.533252

(nwt.2006.2.g <- vegetarian::d(nwt.2006, lev = "gamma", q = 2))

## [1] 15.598

```

Variation Partitioning

We can also partition community variation into proportions explained by variation in spatial (e.g., x and y coordinates) and environmental (e.g., elevation) variables.

To represent spatial variation we'll use the spatial eigenfunction framework, Moran's eigenvector maps (MEMs) [Dray et al., 2006]. In particular, we'll use a special case known as Principal Coordinates of Neighbor Matrices (PCNM), which maps spatial structures from broad to fine scales using a combination of different sine waves [Borcard and Legendre, 2002, Borcard et al. [2004]].

```

# Construct the spatial matrix
nwt.xy.dist <- dist(nwt.xy[,2:3])
nwt.pcnm <- vegan::pcnm(nwt.xy.dist, dist.ret = T)
nwt.pcnm <- scores(nwt.pcnm)[,which(nwt.pcnm$values > 0)]
nwt.pcnm <- as.data.frame(nwt.pcnm)

# Construct the "environmental" matrix
nwt.env <- as.data.frame(nwt.xy[,4]) # elevation
colnames(nwt.env) <- "elevation"

# We can Hellinger-transform the community data for use with RDA
nwt.2006.hel <- decostand(nwt.2006, method = "hellinger")

```

Now, we can perform variation partitioning. Let's use the Hellinger-transformed data first and perform a traditional redundancy analysis (RDA). RDA preserves Euclidean distances, and the Hellinger transformation maintains ecological relevance [Legendre and Gallagher, 2001].

```

(nwt.2006.varpart <- vegan::varpart(nwt.2006.hel, nwt.env, nwt.pcnm))

##
## Partition of variance in RDA
##
## Call: vegan::varpart(Y = nwt.2006.hel, X = nwt.env, nwt.pcnm)

```

```
##
## Explanatory tables:
## X1:  nwt.env
## X2:  nwt.pcnm
##
## No. of explanatory tables: 2
## Total variation (SS): 58.1
##           Variance: 0.66781
## No. of observations: 88
##
## Partition table:
##           Df R.squared Adj.R.squared Testable
## [a+b] = X1      1  0.03695      0.02575    TRUE
## [b+c] = X2     62  0.76040      0.16618    TRUE
## [a+b+c] = X1+X2 63  0.77395      0.18058    TRUE
## Individual fractions
## [a] = X1|X2      1           0.01440    TRUE
## [b]              0           0.01135   FALSE
## [c] = X2|X1     62           0.15484    TRUE
## [d] = Residuals           0.81942   FALSE
## ---
## Use function 'rda' to test significance of fractions of interest
```

Elements of Metacommunity Structure

Now, we will use incidence matrices for the EMS framework. The EMS framework uses co-occurrence patterns to characterize metacommunity structure by identifying coherence (i.e., how discontinuous are species distributions), turnover (i.e., how different is community composition across sites), and boundary clumping (i.e., is turnover gradual or punctuated?). The patterns are then characterized as checkerboard, Clementsian, Gleasonian, nested distributions, and evenly spaced (random) [Leibold and Mikkelsen, 2002, Presley et al. [2010]].

```
ems.2006 <- Metacommunity(
  decostand(nwt.2006[-which(rowSums(nwt.2006) == 0),], method = "pa"),
  method = "r1", sims = 100)
str(ems.2006)

## List of 4
## $ Comm      : num [1:87, 1:71] 0 0 0 0 0 0 0 0 0 0 ...
## .. attr(*, "dimnames")=List of 2
## .. ..$ : chr [1:87] "56" "76" "66" "65" ...
## .. ..$ : chr [1:71] "PAPU2" "ALGE" "PHPU5" "TEGR3" ...
## $ Coherence: Named chr [1:6] "2309" "6.61858260694072" "3.62659232973915e-11" "3556.44" ...
## .. attr(*, "names")= chr [1:6] "embAbs" "z" "pval" "simulatedMean" ...
## $ Turnover : Named chr [1:6] "682728" "-7.21825777169194" "5.2657830713441e-13" "233115.3" ...
## .. attr(*, "names")= chr [1:6] "turnover" "z" "pval" "simulatedMean" ...
## $ Boundary : 'data.frame':  1 obs. of  3 variables:
## ..$ index: num 9.92
## ..$ P      : num 0
## ..$ df      : num 68
IdentifyStructure(ems.2006)

## [1] "Checkerboard (negative coherence)"
```

Metacommunity analyses across a time series

Now, we can repeat these analyses across the long-term datasets and identify shifts in the local versus among-site diversity, the relative importance of metacommunity processes, and species distribution patterns.

```
# This function accepts wide-format dataset and prints analysis output
fn.mc.loop <- function(comm.wide = comm.wide, output = output){

  for(year.i in unique(comm.wide$year)){
    comm.year <- filter(comm.wide, year == year.i)[-c(1:2)] # remove plot & year cols

    # Diversity Partitioning
    comm.year.0.a <- vegetarian::d(comm.year, lev = "alpha", q = 0)
    comm.year.0.b <- vegetarian::d(comm.year, lev = "beta", q = 0)
    comm.year.0.g <- vegetarian::d(comm.year, lev = "gamma", q = 0)

    comm.year.1.a <- vegetarian::d(comm.year, lev = "alpha", q = 1)
    comm.year.1.b <- vegetarian::d(comm.year, lev = "beta", q = 1)
    comm.year.1.g <- vegetarian::d(comm.year, lev = "gamma", q = 1)

    comm.year.2.a <- vegetarian::d(comm.year, lev = "alpha", q = 2)
    comm.year.2.b <- vegetarian::d(comm.year, lev = "beta", q = 2)
    comm.year.2.g <- vegetarian::d(comm.year, lev = "gamma", q = 2)

    # Variation Partitioning
    comm.year.hel <- decostand(comm.year, method = "hellinger")
    comm.year.varpart <- vegan::varpart(comm.year.hel, nwt.env, nwt.pcnm)
    vp <- vector(length = 4)
    vp <- comm.year.varpart$part$indfract$Adj.R.squared
    vp.a <- vp[1]
    vp.b <- vp[2]
    vp.c <- vp[3]
    vp.d <- vp[4]

    # EMS
    comm.year.pa <- decostand(comm.year, method = "pa")
    comm.year.pa <- comm.year.pa[,which(colSums(comm.year.pa) > 0)] # remove empty cols and rows
    comm.year.pa <- comm.year.pa[which(rowSums(comm.year.pa) > 0),]
    ems.year <- Metacommunity(
      comm.year.pa,
      method = "r1", sims = 100)
    comm.year.ems.struc <- (IdentifyStructure(ems.year)) # prints the structure of the MC

    # Write Output
    site.output <- c(year.i,
                     comm.year.0.a, comm.year.0.b, comm.year.0.g,
                     comm.year.1.a, comm.year.1.b, comm.year.1.g,
                     comm.year.2.a, comm.year.2.b, comm.year.2.g,
                     vp.a, vp.b, vp.c, vp.d, comm.year.ems.struc)

    # print(site.output)
    output[which(rownames(output) == year.i), ] <- site.output
  }
  return(output)
}
```

```
}
```

Now, call the function:

```
# Create summary data frame
nwt.time.series <- data.frame(year = unique(nwt.comm.wide$year),
                              d.0.a = NA, d.0.b = NA, d.0.g = NA,
                              d.1.a = NA, d.1.b = NA, d.1.g = NA,
                              d.2.a = NA, d.2.b = NA, d.2.g = NA,
                              vp.a = NA, vp.b = NA, vp.c = NA, vp.d = NA,
                              ems.struc = NA)

rownames(nwt.time.series) <- nwt.time.series$year

mc.time.series.summary <- fn.mc.loop(comm.wide = nwt.comm.wide, output = nwt.time.series)
print(mc.time.series.summary)
```

```
##      year      d.0.a      d.0.b d.0.g      d.1.a
## 1989 1989 9.84090909090909 7.21478060046189    71 4.52670040614776
## 1990 1990 10.7386363636364 6.7047619047619    72 4.93980792173935
## 1995 1995 10.4318181818182 7.18954248366013    75 5.26266590454686
## 1997 1997 11.1590909090909 6.27291242362525    70 5.38836742319992
## 2006 2006      11.5 6.17391304347826    71 5.46484089132516
## 2008 2008 11.5681818181818 6.13752455795678    71 5.61559416896894
## 2010 2010 11.5454545454545 6.40944881889764    74 5.50964667607385
## 2011 2011 11.3977272727273 6.84346959122632    78 5.42396565205511
## 2012 2012 11.9431818181818 6.61465271170314    79 5.7426636535779
## 2013 2013 12.5340909090909 6.54215775158658    82 6.10546184026241
## 2014 2014 12.1704545454545 6.40896358543417    78 6.0104706081435
##      d.1.b      d.1.g      d.2.a      d.2.b
## 1989 4.60930789926233 20.8649559396508 2.77833881861833 4.61436475957228
## 1990 4.11311310256979 20.3179886870841 3.12502563309585 4.02937671030435
## 1995 4.10427614540651 21.5994341332758 3.27100730968259 3.91714113319974
## 1997 4.15279691531311 22.3767956136383 3.2793508152403 4.25870250858984
## 2006 4.49337681923025 24.555589381862 3.44079656265581 4.53325163779928
## 2008 4.48808811509123 25.2032814489251 3.50948486633673 4.52327782391778
## 2010 4.42775173497514 24.395347629086 3.41863022744422 4.54698746868182
## 2011 4.48572267086086 24.3304056913942 3.40081859783568 4.48493437052737
## 2012 4.40371461064094 25.2890518352576 3.53656487535522 4.43767713549471
## 2013 4.4212007527204 26.9934724838739 3.78069527535298 4.52057559017015
## 2014 4.3819014232647 26.3372897123146 3.72951844250882 4.38214394188651
##      d.2.g      vp.a      vp.b
## 1989 12.8202687347841 0.0294520349422486 0.00186417219900992
## 1990 12.5919055051005 0.0320876503704703 -0.00731368641607755
## 1995 12.8129972797547 0.01479721657823 0.016441312467207
## 1997 13.96577954341 0.0240744953314578 0.00537931111068191
## 2006 15.5979966529936 0.0144011582464573 0.0113455852809493
## 2008 15.874375069276 0.0162096652438097 0.0111325468165616
## 2010 15.5444688042457 0.0159612899327055 0.0105345252150492
## 2011 15.2524482173619 0.0215279819736879 0.0102723221937753
## 2012 15.6941330855576 0.0131751888711407 0.0174700164372711
## 2013 17.0909187756323 0.0173542657525155 0.0100963856637064
## 2014 16.3432866489941 0.0174204354538076 0.00703275027300088
##      vp.c      vp.d      ems.struc
## 1989 0.133959225217372 0.834724567641369 Checkerboard (negative coherence)
## 1990 0.130687688790609 0.844538347254999 Checkerboard (negative coherence)
```

```
## 1995 0.094343470476594 0.874418000477969 Checkerboard (negative coherence)
## 1997 0.125317647933692 0.845228545624168 Checkerboard (negative coherence)
## 2006 0.154837696173837 0.819415560298756 Checkerboard (negative coherence)
## 2008 0.182274727398227 0.790383060541402 Checkerboard (negative coherence)
## 2010 0.171691856098228 0.801812328754017 Checkerboard (negative coherence)
## 2011 0.185219370672602 0.782980325159935 Checkerboard (negative coherence)
## 2012 0.158116588928553 0.811238205763036 Checkerboard (negative coherence)
## 2013 0.186724184734312 0.785825163849467 Checkerboard (negative coherence)
## 2014 0.161877606808657 0.813669207464534 Checkerboard (negative coherence)
```

References

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