### COMMUNITY DATA ANALYSIS USING VEGAN

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#### MATERIALS

Handouts and all the sources are on github:

github.com/gavinsimpson/UBCVeganStudyGroup



#### CANONICAL CORRESPONDENCE ANALYSIS

CCA is the constrained form of CA; fitted using cca()

Finds axes that are linear combinations of the explanatory variables

Two interfaces for specifying models

- basic; cca1 <- cca(X = varespec, Y = varechem)</pre>
- formula; cca1 <- cca(varespec ~ ., data = varechem)</pre>

Formula interface is the more powerful — recommended

#### CANONICAL CORRESPONDENCE ANALYSIS

```
cca1 <- cca(varespec ~ ., data = varechem)</pre>
cca1
Call: cca(formula = varespec ~ N + P + K + Ca + Mg + S + Al + Fe +
Mn + Zn + Mo + Baresoil + Humdepth + pH, data = varechem)
             Inertia Proportion Rank
Total
            2.0832 1.0000
Constrained 1.4415 0.6920 14
Unconstrained 0.6417 0.3080
Inertia is mean squared contingency coefficient
Eigenvalues for constrained axes:
 CCA1 CCA2 CCA3 CCA4 CCA5 CCA6 CCA7 CCA8 CCA9 CCA10
0 4389 0 2918 0 1628 0 1421 0 1180 0 0890 0 0703 0 0584 0 0311 0 0133
CCA11 CCA12 CCA13 CCA14
0.0084 0.0065 0.0062 0.0047
Eigenvalues for unconstrained axes:
   CA1
           CA2
                   CA3
                          CA4
                                 CA5
                                         CA6
0.19776 0.14193 0.10117 0.07079 0.05330 0.03330 0.01887 0.01510 0.00949
```

#### REDUNDANCY ANALYSIS

RDA is the constrained form of PCA; fitted using rda().

```
rda1 <- rda(varespec ~ .. data = varechem)
rda1
Call: rda(formula = varespec ~ N + P + K + Ca + Mg + S + Al + Fe +
Mn + Zn + Mo + Baresoil + Humdepth + pH. data = varechem)
               Inertia Proportion Rank
Total
            1825.6594
                         1.0000
Constrained 1459.8891
                       0.7997 14
Unconstrained 365,7704
                         0.2003 9
Inertia is variance
Eigenvalues for constrained axes:
RDA1 RDA2 RDA3 RDA4 RDA5 RDA6
                                  RDA7 RDA8 RDA9 RDA10 RDA11 RDA12
820.1 399.3 102.6 47.6 26.8 24.0 19.1 10.2 4.4 2.3 1.5 0.9
RDA13 RDA14
 0.7 0.3
Eigenvalues for unconstrained axes:
  PC1
         PC2
               PC3
                      PC4
                             PC5
                                   PC6
                                          PC7
                                                       PC9
186.19 88.46 38.19 18.40 12.84 10.55
                                        5.52 4.52 1.09
```

#### **EIGENVALUES**

Use eigenvals() to extract Eigenvalues from a fitted ordination object

```
eigenvals(cca1)
```

```
CCA1
               CCA2
                         CCA3
                                   CCA4
                                              CCA5
                                                        CCA6
                                                                  CCA7
0.4388704 0.2917753 0.1628465 0.1421302 0.1179519 0.0890291 0.0702945
     CCA8
               CCA9
                        CCA10
                                  CCA11
                                             CCA12
                                                       CCA13
                                                                 CCA14
0.0583592 0.0311408 0.0132944 0.0083644 0.0065385 0.0061563 0.0047332
      CA1
                CA2
                          CA3
                                    CA4
                                               CA5
                                                         CA6
                                                                   CA7
0.1977645 0.1419256 0.1011741 0.0707868 0.0533034 0.0332994 0.0188676
      CA8
                CA9
0.0151044 0.0094876
```

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#### **EIGENVALUES**

# summary() method for eigenvals() shows more information

summarv(eigenvals(cca1. constrained = TRUE))

Cumulative Proportion 1.000000

```
Importance of components:
                       CCA1
                              CCA2
                                     CCA3 CCA4
                                                     CCA5
                                                             CCA6
                                                                     CCA7
Eigenvalue
                     0.4389 0.2918 0.1628 0.1421 0.11795 0.08903 0.07029
Proportion Explained
                     0.3045 0.2024 0.1130 0.0986 0.08183 0.06176 0.04877
Cumulative Proportion 0.3045 0.5069 0.6198 0.7184 0.80027 0.86203 0.91080
                         CC\Delta 8
                                 CCA9 CCA10
                                                 CCA11
                                                          CCA12
                                                                   CCA13
Eigenvalue
                     0.05836 0.03114 0.01329 0.008364 0.006538 0.006156
Proportion Explained
                     0.04049 0.02160 0.00922 0.005800 0.004540 0.004270
Cumulative Proportion 0.95128 0.97288 0.98211 0.987910 0.992450 0.996720
                         CCA14
Eigenvalue
                     0.004733
Proportion Explained
                     0.003280
```

#### **EXTRACTING AXIS SCORES**

To extract a range of scores from a fitted ordination use scores()

- takes an ordination object as the first argument
- choices which axes? Defaults to c(1,2)
- display which type(s) of scores to return
  - · "sites" or "wa": scores for samples in response matrix
  - "species": scores for variables/columns in response
  - · "lc": linear combination site scores
  - "bp": biplot scores (coords of arrow tip)
  - · "cn": centroid scores (coords of factor centroids)

#### **EXTRACTING AXIS SCORES**

```
str(scores(cca1, choices = 1:4, display = c("species", "sites")), max = 1)
list of 2
 $ species: num [1:44, 1:4] 0.0753 -0.1813 -1.0535 -1.2774 -0.1526 ...
  ..- attr(*, "dimnames")=List of 2
 $ sites : num [1:24, 1:4] 0.178 -0.97 -1.28 -1.501 -0.598 ...
  ..- attr(*. "dimnames")=List of 2
head(scores(cca1, choices = 1:2, display = "sites"))
        CCA1
               CCA2
18 0.1784733 -1.0598842
15 -0.9702382 -0.1971387
24 -1.2798478 0.4764498
27 -1.5009195 0.6521559
23 -0.5980933 -0.1840362
19 -0.1102881 0.7143142
```

#### SCALINGS...

When we draw the results of many ordinations we display 2 or more sets of data

Can't display all of these and maintain relationships between the scores

Solution scale one set of scores relative to the other via the scaling argument

- · scaling = 1 Focus on sites, scale site scores by  $\lambda_i$
- $\cdot$  scaling = 2 Focus on species, scale species scores by  $\lambda_i$
- $\cdot$  scaling = 3 Symmetric scaling, scale both scores by  $\sqrt{\lambda_i}$
- $\cdot$  scaling = -1 As above, but
- scaling = -2 For cca() multiply results by  $\sqrt{(1/(1-\lambda_i))}$
- scaling = -3 this is Hill's scaling
- scaling < 0 For rda() divide species scores by species'  $\sigma$
- scaling = 0 raw scores

```
scores(cca1, choices = 1:2, display = "species", scaling = 3)
```

#### SCALINGS...

From vegan version 2.3-1 we have a simpler way to select the type of scaling scaling can be a character vector indicating the broad type of scaling required

- · "species"
- · "sites"
- · "symmetric"
- · "none"

A second argument then allows selection of the relevant negative scaling type:

- · correlation = TRUE for linear methods
- hill = TRUE for unimodal methods

#### PARTIAL CONSTRAINED ORDINATIONS

Partial constrained ordinations remove the effect of one or more variables then fit model of interest

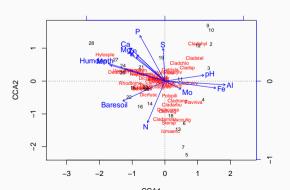
Argument Z is used for a data frame of variables to partial out

Or with the formula interface use the Condition() function

#### **TRIPLOTS**

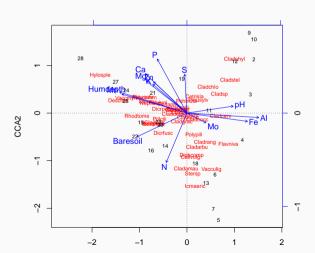
Triplots will generally produce a mess; we can really only display a couple of bits approximately anyway Trying to cram three things in is a recipe for a mess... but we can do it

plot(cca1)



## **TRIPLOTS**

plot(cca1)



#### BUILDING CONSTRAINED ORDINATION MODELS

If we don't want to think it's easy to fit a poor model with many constraints

That's what we just did with cca1 and rda1

Remember, CCA and RDA are *just regression methods* — everything you know about regression applies here

A better approach is to *think* about the important variables and include only those

The formula interface allows you to create interaction or quadratic terms easily (though be careful with latter)

It also handles factor or class constraints automatically unlike the basic interface

#### **BUILDING CONSTRAINED ORDINATION MODELS**

```
vare.cca <- cca(varespec ~ Al + P*(K + Baresoil), data = varechem)
vare.cca
Call: cca(formula = varespec \sim Al + P * (K + Baresoil). data =
varechem)
            Inertia Proportion Rank
Total
         2.083 1.000
Constrained 1.046 0.502 6
Unconstrained 1.038 0.498 17
Inertia is mean squared contingency coefficient
Eigenvalues for constrained axes:
 CCA1 CCA2 CCA3 CCA4 CCA5 CCA6
0.3756 0.2342 0.1407 0.1323 0.1068 0.0561
Eigenvalues for unconstrained axes:
   CA1
           CA2
                  CA3 CA4 CA5 CA6 CA7
                                                       CA8
0.27577 0.15411 0.13536 0.11803 0.08887 0.05511 0.04919 0.03781
(Showed only 8 of all 17 unconstrained eigenvalues)
```

#### **BUILDING CONSTRAINED ORDINATION MODELS**

For CCA we have little choice but to do

- 1. Fit well-chosen set of candidate models & compare, or
- 2. Fit a full model of well-chosen variables & then do stepwise selection

But automatic approaches to model building should be used cautiously!

The standard step() function can be used as vegan provides two helper methods, deviance() and extractAIC(), used by step()

Vegan also provides methods for class "cca" for add1() and drop1()

#### STEPWISE SELECTION IN CCA

step() uses AIC which is a fudge for RDA/CCA. Alternatively use function ordistep()

- 1. Define an upper and lower model scope, say the full model and the null model
- 2. To step from the lower scope or null model we use

```
upr <- cca(varespec ~ ., data = varechem)
lwr <- cca(varespec ~ 1, data = varechem)
set.seed(1)
mods <- ordistep(lwr, scope = formula(upr), trace = 0)</pre>
```

trace = 0 is used her to turn off printing of progress

Permutation tests are used (more on these later); the theory for an AIC for ordination is somewhat loose

mods

The object returned by ordistep() is a standard "cca" object with an extra component \$anova

```
Call: cca(formula = varespec ~ Al + P + K, data = varechem)
             Inertia Proportion Rank
Total
              2.0832
                       1.0000
Constrained
              0.6441 0.3092
Unconstrained 1.4391 0.6908
                                 20
Inertia is mean squared contingency coefficient
Eigenvalues for constrained axes:
 CCA1 CCA2 CCA3
0.3616 0.1700 0.1126
Eigenvalues for unconstrained axes:
         CA2
                CA3
                       CA4
                             CA5
                                    CA6
                                           CA7
0.3500 0.2201 0.1851 0.1551 0.1351 0.1003 0.0773 0.0537
(Showed only 8 of all 20 unconstrained eigenvalues)
```

#### STEPWISE SELECTION IN CCA

The **\$anova** component contains a summary of the steps involved in automatic model building

#### mods\$anova

```
Df AIC F Pr(>F)
+ Al 1 128.61 3.6749 0.005 **
+ P 1 127.91 2.5001 0.005 **
+ K 1 127.44 2.1688 0.035 *
---
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

#### STEPWISE SELECTION IN CCA

Step-wise model selection is fairly fragile; if we start from the full model we won't end up with the same final model

```
mods2 <- ordistep(upr, scope = list(lower = formula(lwr), upper = formula(upr)), trace = 0)</pre>
mods2
Call: cca(formula = varespec ~ P + K + S + Mo + Baresoil +
Humdepth. data = varechem)
             Inertia Proportion Rank
              2.0832
                      1.0000
Total
Constrained
              0.9377 0.4501
Unconstrained 1.1455 0.5499 17
Inertia is mean squared contingency coefficient
Eigenvalues for constrained axes:
 CCA1 CCA2 CCA3 CCA4 CCA5 CCA6
0.3712 0.2356 0.1364 0.0974 0.0813 0.0159
Eigenvalues for unconstrained axes:
   CA1
         CA2
                CA3
                       CA4
                              CA5
                                     CAG
0.3295 0.1893 0.1548 0.1269 0.0968 0.0616 0.0464 0.0337
(Showed only 8 of all 17 unconstrained eigenvalues)
```

# ADJUSTED $\it r^2$ FOR $\it LINEAR$ MODELS

As with ordinary  $\mathbb{R}^2$ , that of an RDA is biased for the same reasons as for a linear regression

- $\cdot$  adding a variable to constraints will increase  $R^2$
- the larger the number of constraints in the model the larger  $\mathbb{R}^2$  is due to random correlations

Can attempt to account for this bias via an adjusted  $\mathbb{R}^2$  measure

$$R_{adj}^2 = 1 - \frac{n-1}{n-m-1}(1-R^2)$$

- $\cdot$  n is number of samples m is number of constraints (model degrees of freedom)
- Can be used up to  $\sim M > n/2$  before becomes too conservative
- Can be negative
- Compute using RsquareAdj()

# STEPWISE SELECTION VIA ADJUSTED $\it r^2$

The problems with stepwise selection in regression models are myriad. Affects RDA, CCA, etc as well

Blanchet, Legendre, and Borcard (2008) proposed a two-step solution for models where  $R^2_{adj}$  makes sense

- · Global test of all constraints
  - · Proceed only if this test is significant
  - Helps prevent inflation of overall type I error
- · Proceed with forward selection, but with two stopping rules
  - $\cdot$  Usual significance threshold lpha
  - The global  $R_{adj}^2$
  - · Stop if next candidate model is non-significant or if  $R^2_{adj}$  exceeds the global  $R^2_{adj}$

### Available in ordiR2step()



#### PERMUTATION TESTS IN VEGAN

RDA has lots of theory behind it, CCA not as much. However, ecological/environmental data invariably violate what little theory we have

Instead we use permutation tests to assess the importance of fitted models — the data are shuffled in some way and the model refitted to derive a Null distribution under some hypothesis of  $no\ effect$ 

#### PERMUTATION TESTS IN VEGAN

What is shuffled and how is of paramount importance for the test to be valid

- If no conditioning (partial) variables then rows of the species data are permuted
- With conditioning variables, two options are available, both of which permute residuals from model fits
  - The *full model* uses residuals from model  $Y = X + Z + \varepsilon$
  - The reduced model uses residuals from model  $Y = Z + \varepsilon$
- In vegan which is used can be set via argument model with "direct", "full", and "reduced" respectively
- In current vegan option method = "full" is disabled

#### PERMUTATION TESTS IN VEGAN

A test statistic is required, computed for observed model & each permuted model vegan uses a pseudo-F statistic

$$F = \frac{\chi^2_{model}/df_{model}}{\chi^2_{resid}/df_{resid}}$$

Evaluate whether  $\it{F}$  is unusually large relative to the null (permutation) distribution of  $\it{F}$ 

# PERMUTATION TESTS IN VEGAN: anova()

- The main user function is the anova() method
- It is an interface to the lower-level function permutest.cca()
- At its most simplest, the anova() method tests whether the "model" as a whole is significant

$$F = \frac{1.4415/14}{0.6417/9} = 1.4441$$

## DETAILS ON THE PERMUTATIONS — permustats

To get details on the permutations use permustats()

```
pstat <- permustats(perm)
summary(pstat)

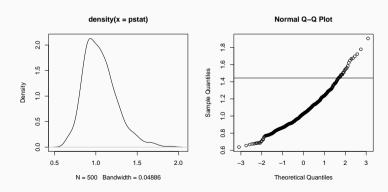
statistic SES mean lower median upper
Model 1.4441 1.9675 1.0513 1.0266 1.4190

(Interval (Upper - Lower) = 0.95)</pre>
```

# DETAILS ON THE PERMUTATIONS — permustats

To get details on the permutations use permustats()

```
layout(matrix(1:2, ncol = 2))
plot(density(pstat))
qqnorm(pstat)
layout(1)
```



# PERMUTATION TESTS IN VEGAN: anova()

# anova.cca() has a number of arguments

```
function (object, ..., permutations = how(nperm = 999), by = NULL,
    model = c("reduced", "direct", "full"), parallel = getOption("mc.cores"),
    strata = NULL, cutoff = 1, scope = NULL)
NULL
```

- permutations controls the permutation test; one of
  - 1. a number of (unrestricted) permutations to do
  - 2. a matrix of pre-generated permutations
  - 3. an object returned by how()
- · by determines what is tested; the default is to test the model
- More direct control can be achieved via permutest.cca()
- parallel allows for running the permutations on multiple CPU cores

#### TYPES OF PERMUTATION TEST IN VEGAN

A number of types of test can be envisaged

- Testing the overall significance of the model
- Testing constrained (canonical) axes
- Testing individual model terms sequentially
- The marginal effect of a single variable

The first is the default in anova()

The other three can be selected via the argument by

### PERMUTATION TESTS | TESTING CANONICAL AXES

- The constrained (canonical) axes can be individually tests by specifying by = "axis"
- The first axis is tested in terms of variance explained compared to residual variance
- The second axis is tested after partialling out the first axis... and so on

```
set.seed(1)
anova(mods, by = "axis", permutations = 499)
Permutation test for cca under reduced model
Marginal tests for axes
Permutation: free
Number of permutations: 499
Model: cca(formula = varespec ~ Al + P + K. data = varechem)
        Df ChiSquare
                          F Pr(>F)
CCA1
             0.36156 5.0249 0.002 **
     1 0.16996 2.3621 0.014 *
CCA2
      1 0.11262 1.5651 0.114
CCA3
Residual 20 1.43906
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

## PERMUTATION TESTS | TESTING TERMS SEQUENTIALLY

- The individual terms in the model can be tested using by = "terms"
- The terms are assessed in the order they were specified in the model, sequentially from first to last
- Test is of the additional variance explained by adding the kth variable to the model
- Ordering of the terms will affect the results

### PERMUTATION TESTS | TESTING TERMS MARGINAL EFFECTS

- The marginal effect of a model term can be assessed using by = "margin"
- The marginal *effect* is the effect of a particular term when all other model terms are included in the model

```
set.seed(10)
anova(mods, by = "margin", permutations = 499)
Permutation test for cca under reduced model
Marginal effects of terms
Permutation: free
Number of permutations: 499
Model: cca(formula = varespec ~ Al + P + K. data = varechem)
        Df ChiSquare
                          F Pr(>F)
Δ1
         1 0.31184 4.3340 0.002 **
        1 0 16810 2 3362 0 014 +
        1 0.15605 2.1688 0.032 *
Residual 20 1.43906
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Example & data taken from Leps & Smilauer, Case Study 2

Spring fen meadow vegetation in westernmost Carpathian mountains

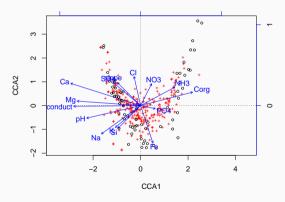
```
## load vegan
library("vegan")

## load the data
spp <- read.csv("data/meadow-spp.csv", header = TRUE, row.names = 1)
env <- read.csv("data/meadow-env.csv", header = TRUE, row.names = 1)</pre>
```

CCA a reasonable starting point as the gradient is long here (check with **decorana()** if you want)

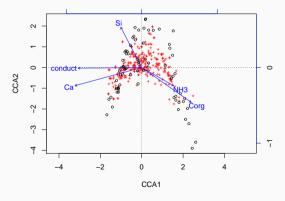
```
m1 < -cca(spp \sim ., data = env)
set.seed(32)
anova(m1. permutations = 499)
Permutation test for cca under reduced model
Permutation: free
Number of permutations: 499
Model: cca(formula = spp ~ Ca + Mg + Fe + K + Na + Si + SO4 + PO4 + NO3 + NH3 + Cl + Corg + pH + conduct + slope
         Df ChiSquare F Pr(>F)
Model 15 1.5597 1.497 0.002 **
Residual 54 3.7509
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

plot(m1)



```
set.seed(67)
lwr < -cca(spp ~ 1. data = env)
m2 <- ordistep(lwr. scope = formula(m1), trace = FALSE, permutations = 99)
m2
Call: cca(formula = spp ~ Ca + conduct + Corg + NH3 + Si, data =
env)
             Inertia Proportion Rank
Total
              5.3107
                      1 0000
Constrained
              0.8034
                      0.1513
Unconstrained 4.5073 0.8487 64
Inertia is mean squared contingency coefficient
Eigenvalues for constrained axes:
 CCA1 CCA2 CCA3 CCA4 CCA5
0.4221 0.1195 0.1036 0.0807 0.0775
Eigenvalues for unconstrained axes:
    CA1
           CA2
                   CA3
                           CA4
                                  CA5
                                          CA6
                                                  CA7
0.29763 0.19604 0.17163 0.15357 0.14613 0.14229 0.13519 0.12476
(Showed only 8 of all 64 unconstrained eigenvalues)
```

plot(m2)



#### m2\$anova

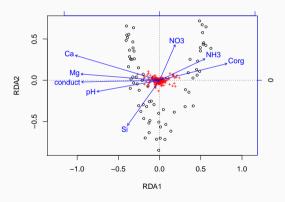
```
Df AIC F Pr(>F)
+ Ca 1 453.14 4.7893 0.01 **
+ conduct 1 453.29 1.7915 0.01 **
+ Corg 1 453.61 1.6011 0.01 **
+ NH3 1 453.96 1.5533 0.01 **
+ Si 1 454.42 1.4231 0.01 **

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

#### Alternative is RDA with a transformation

```
spph <- decostand(spp, method = "hellinger")
m3 <- rda(spph ~ ., data = env)
lwr <- rda(spph ~ 1, data = env)
m4 <- ordistep(lwr, scope = formula(m3), trace = FALSE, permutations = 99)</pre>
```

plot(m4)



# Stepwise using $R^2_{\it adj}$

```
m5 <- ordiR2step(lwr, scope = formula(m3), trace = FALSE, permutations = 99)
m5$anova</pre>
```

#### DIAGNOSTICS FOR CONSTRAINED ORDINATIONS

**vegan** provides a series of diagnostics to help assess the model fit

- goodness()
- · inertcomp()
- · spenvcor()
- · intersetcor()
- · vif.caa()



#### RESTRICTED PERMUTATION TESTS

What is shuffled and how is of paramount importance for the test to be valid

Complete randomisation (default in **vegan**) assumes a null hypothesis where all observations are *independent* 

Ecological / environmental data often aren't independent

- Temporal or spatial correlation
- · Clustering, repeated measures
- Nested sampling designs (Split-plots designs)
- Blocks
- ...

Permutation *must* give null distribution of the test statistic whilst preserving the *dependence* between observations

Trick is to shuffle the data whilst preserving that dependence

#### RESTRICTED PERMUTATIONS

Canoco has had restricted permutations for a *long* time. **vegan** has only recently caught up & we're not (quite) there yet

**vegan** used to only know how to completely randomise data or completely randomise within blocks (via **strata** in **vegan**)

The newish package **permute** grew out of initial code in the **vegan** repository to generate the sorts of restricted permutations available in Canoco

We have now fully integrated **permute** into **vegan**...

vegan depends on permute so it will already be installed & loaded when using vegan

#### RESTRICTED PERMUTATIONS WITH PERMUTE

**permute** follows Canoco closely — at the chiding of Cajo ter Braak when it didn't do what he wanted!

Samples can be thought of as belonging to three levels of a hierarchy

- the sample level; how are individual samples permuted
- the *plot* level; how are samples grouped at an intermediate level
- the *block* level; how are samples grouped at the outermost level

Blocks define groups of plots, each of which can contain groups of samples

#### RESTRICTED PERMUTATIONS WITH PERMUTE

Blocks are *never* permuted; if defined, only plots or samples *within* the blocks get shuffled & samples are **never** swapped between blocks

Plots or samples within plots, or both can be permuted following one of four simple permutation types

- 1. Free permutation (randomisation)
- 2. Time series or linear transect, equal spacing
- 3. Spatial grid designs, equal regular spacing
- 4. Permutation of plots (groups of samples)
- 5. Fixed (no permutation)

Multiple plots per block, multiple samples per plot; plots could be arranged in a spatial grid and samples within each of the plots form a time series

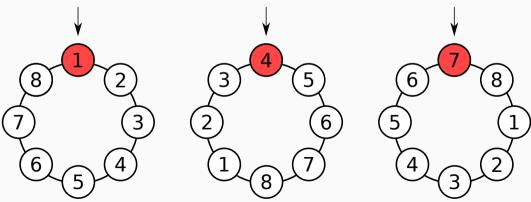
#### RESTRICTED PERMUTATIONS WITH PERMUTE | BLOCKS

- Blocks are a random factor that does not interact with factors that vary within blocks
- Blocks form groups of samples that are never permuted between blocks, only within blocks
- Using blocks you can achieve what the **strata** argument used to in **vegan**; needs to be a factor variable
- The variation *between* blocks should be excluded from the test; **permute** doesn't do this for you!
- Use + Condition(blocks) in the model formula where blocks is a factor containing the block membership for each observation

### RESTRICTED PERMUTATIONS WITH PERMUTE | TIME SERIES & LINEAR TRANSECTS

Can *randomly* link starting point of one series to any time point of another series if series are stationary under null hypothesis that the series are unrelated

Achieve this via cyclic shift permutations — wrap series into a circle by joining start and end points



#### RESTRICTED PERMUTATIONS WITH PERMUTE | TIME SERIES & LINEAR TRANSECTS

Works OK if there are no trends or cyclic pattern — autocorrelation structure only broken at the end points if series are stationary

Can detrend to make series stationary but not if you want to test significance of a trend

```
shuffle(10, control = how(within = Within(type = "series")))
[1] 10  1  2  3  4  5  6  7  8  9
```

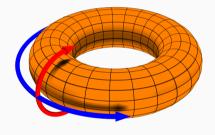
#### RESTRICTED PERMUTATIONS WITH PERMUTE | SPATIAL GRIDS

The trick of cyclic shifts can be extended to two dimensions for a regular spatial grid arrangement of points

Now shifts are *toroidal* as we join the end point in the *x* direction together and in the *y* direction together

```
matrix(perm, ncol = 3)
```

	[,1]	[,2]	[,3]
[1,]	6	9	3
[2,]	4	7	1
[3,]	5	8	2



Source: Dave Burke, Wikimedia 💩 🕦

#### RESTRICTED PERMUTATIONS WITH PERMUTE | WHOLE-PLOTS & SPLIT-PLOTS I

Split-plot designs are hierarchical with two levels of units

- 1. whole-plots, which contain
- 2. split-plots (the samples)

Can permute one or both of these but whole-plots must be of equal size

Essentially allows more than one error stratum to be analyzed

Test effect of constraints that vary *between* whole plots by permuting the whole-plots whilst retaining order of split-splots (samples) within the whole-plots

Test effect of constraints that vary within whole-plots by permuting the split-plots within whole-plots without permuting the whole-plots

### RESTRICTED PERMUTATIONS WITH PERMUTE | WHOLE-PLOTS & SPLIT-PLOTS II

Whole-plots or split-plots can be time series, linear transects or rectangular grids in which case the appropriate restricted permutation is used

If the split-plots are parallel time series & time is an autocorrelated error component affecting all series then the same cyclic shift can be applied to each time series (within each whole-plot) (constant = TRUE)

#### RESTRICTED PERMUTATIONS WITH PERMUTE | MIRRORING

(Without wanting to get *too* technical) Mirroring in restricted permutations allows for isotropy in dependencies by reflecting the ordering of samples in time or spatial dimensions

For a linear transect, technically the autocorrelation at lag h is equal to that at lag -h (also in a trend-free time series)

Hence the series (1, 2, 3, 4) and (4, 3, 2, 1) are equivalent fom this point of view & we can draw permutations from either version

Similar argument can be made for spatial grids

Using mirror = TRUE then can double (time series, linear transects) or quadruple (spatial grids) the size of the set of permutations

#### RESTRICTED PERMUTATIONS WITH PERMUTE | THE SET OF PERMUTATIONS

Using restricted permutations can severely reduce the size of the set of allowed permutations

As the minimum p value obtainable is 1/np where np is number of allowed permutations (including the observed) this can impact the ability to detect signal/pattern

If we don't want mirroring

- in a time series of 20 samples the minimum p is 1/20 (0.05)
- in a time series of 100 samples the minimum p is 1/100 (0.01)
- in a data set with 10 time series each of 20 observations (200 total), if we assume an autocorrelated error component over all series (constant = TRUE) then there are only 20 permutations of the data and minimum p is 0.05

When the set of permutations is small it is better to switch to an exact test & evaluate all permutations in the set rather than randomly sample from the set

In permute, we set up a permutation scheme with how()

We sample from the permutation scheme with

- shuffle(), which gives a single draw from scheme, or
- $\cdot$  shuffleSet(), which returns a set of n draws from the scheme

allPerms() can generated the entire set of permutations — note this was designed for small sets of permutations & is slow if you request it for a scheme with many thousands of permutations!

### how( ) has three main arguments

- 1. within takes input from helper Within()
- plots takes input from helper Plots()
- 3. **blocks** takes a factor variable as input

```
plt <- gl(3, 10)
h <- how(within = Within(type = "series"), plots = Plots(strata = plt))</pre>
```

Helper functions make it easy to change one or a few aspects of permutation scheme, rest left at defaults

```
args(Within)

function (type = c("free", "series", "grid", "none"), constant = FALSE,
    mirror = FALSE, ncol = NULL, nrow = NULL)

NULL

args(Plots)

function (strata = NULL, type = c("none", "free", "series", "grid"),
    mirror = FALSE, ncol = NULL, nrow = NULL)

NULL
```

how() has additional arguments, many of which control the heuristics that kick in to stop you shooting yourself in the foot and demanding 9999 permutations when there are only 10

- complete should we enumerate the entire set of permutations?
- minperm lower bound on the size of the set of permutations at & below which we turn on complete enumeration

```
args(how)
```

### RESTRICTED PERMUTATIONS WITH PERMUTE | TIME SERIES EXAMPLE I

Time series within 3 plots, 10 observation each

#### RESTRICTED PERMUTATIONS WITH PERMUTE | TIME SERIES EXAMPLE II

Time series within 3 plots, 10 observation each, same permutation within each

Now we've seen how to drive **permute**, we can use the same **how()** commands to set up permutation designs within **vegan** functions

Analyse the Ohraz data Case study 5 of Leps & Smilauer

Repeated observations of composition from an experiment

- Factorial design (3 replicates)
- · Treatments: fertilisation, mowing, Molinia removal

Test 1 of the hypotheses

There are no directional changes in species composition in time that are common to all treatments or specific treatments

Analyse the Ohraz data Case study 5 of Leps & Smilauer

```
## load the data
spp <- read.csv("data/ohraz-spp.csv", header = TRUE, row.names = 1)
env <- read.csv("data/ohraz-env.csv", header = TRUE, row.names = 1)
molinia <- spp[, 1]
spp <- spp[, -1]
env <- transform(env, year = as.numeric(as.character(year))) # Year as numeric</pre>
```

```
c1 <- rda(spp ~ year + year:mowing + year:fertilizer + year:removal +
              Condition(plotid), data = env)
(h <- how(nperm = 499, within = Within(type = "none").
          plots = with(env, Plots(strata = plotid, type = "free"))))
Permutation Design:
Blocks:
  Defined by: none
Plats.
  Plots: plotid
  Permutation type: free
  Mirrored?: No
Within Plots:
  Permutation type: none
Permutation details:
  Number of permutations requested: 499
  Max. number of permutations allowed: 9999
```

Evaluate all permutations?: No. Activation limit: 99

```
set.seed(23)
anova(c1, permutations = h, model = "reduced")
Permutation test for rda under reduced model
Plots: plotid, plot permutation: free
Permutation: none
Number of permutations: 499
Model: rda(formula = spp ~ year + year:mowing + year:fertilizer + year:removal + Condition(plotid), data =
         Df Variance F Pr(>F)
Model 4 158.85 6.4247 0.002 **
Residual 90 556.30
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
set.seed(24)
anova(c1, permutations = h, model = "reduced", by = "axis")
Permutation test for rda under reduced model
Marginal tests for axes
Plots: plotid, plot permutation: free
Permutation: none
Number of permutations: 499
Model: rda(formula = spp ~ year + year:mowing + year:fertilizer + year:removal + Condition(plotid), data =
        Df Variance F Pr(>F)
RDA1
        1 89.12 14.4173 0.002 **
RDA2 1 34.28 5.5458 0.004 **
RDA3 1 26.52 4.2900 0.004 **
RDA4 1 8.94 1.4458 0.640
Residual 90 556.30
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

#### HIERARCHICAL ANALYSIS OF CRAYFISH

Variation in communities may exist at various scales, sometimes hierarchically A firt step in understanding this variation is to test for its exisistence In this example from Leps & Smilauer (2014) uses crayfish data from Spring River, Arkansas/Missouri, USA, collected by Dr.~Camille Flinders.

567 records of 5 species (each sub-divided into Large & Small individuals

#### HIERARCHICAL ANALYSIS OF CRAYFISH

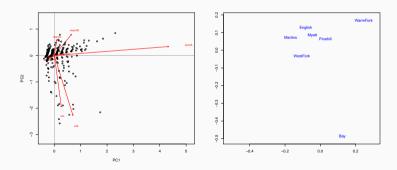
#### HIERARCHICAL ANALYSIS OF CRAYFISH — UNCONSTRAINED

Number of samples have 0 crayfish, which excludes unimodal methods

```
m.pca <- rda(crayfish)</pre>
summary(eigenvals(m.pca))
Importance of components:
                         PC1
                                PC2
                                       PC3
                                               PC4
                                                       PC5
                                                               PC6
                                                                       PC7
Eigenvalue
                      3.5728 1.8007 1.1974 0.9012 0.79337 0.38886 0.28132
Proportion Explained
                      0.3818 0.1924 0.1280 0.0963 0.08478 0.04155 0.03006
Cumulative Proportion 0.3818 0.5742 0.7022 0.7985 0.88325 0.92480 0.95486
                          PC8
                                  PC9
                                           PC10
Eigenvalue
                      0.21225 0.20528 0.004881
Proportion Explained 0.02268 0.02194 0.000520
Cumulative Proportion 0.97754 0.99948 1.000000
```

### HIERARCHICAL ANALYSIS OF CRAYFISH — UNCONSTRAINED

```
layout(matrix(1:2, ncol = 2))
biplot(m.pca, type = c("text", "points"), scaling = "species")
set.seed(23)
ev.pca <- envfit(m.pca ~ Watershed, data = design, scaling = "species")
plot(ev.pca, labels = levels(design$Watershed), add = FALSE)
layout(1)</pre>
```



### HIERARCHICAL ANALYSIS OF CRAYFISH — WATERSHED SCALE

```
m.ws <- rda(crayfish ~ Watershed, data = design)</pre>
m.ws
Call: rda(formula = cravfish ~ Watershed, data = design)
             Inertia Proportion Rank
Total
          9.3580
                         1.0000
Constrained 1.7669 0.1888
Unconstrained 7.5911 0.8112 10
Inertia is variance
Eigenvalues for constrained axes:
  RDA1
         RDA2
                RDA3
                      RDA4
                             RDA5
                                    RDA6
0.7011 0.5540 0.3660 0.1064 0.0381 0.0013
Eigenvalues for unconstrained axes:
   PC1
          PC2
                 PC3
                       PC4
                              PC5
                                     PC6
                                            PC7
                                                   PC8
                                                          PC9
3.0957 1.2109 0.9717 0.7219 0.5333 0.3838 0.2772 0.2040 0.1879 0.0048
```

PC10

### HIERARCHICAL ANALYSIS OF CRAYFISH — WATERSHED SCALE

```
summarv(eigenvals(m.ws. constrained = TRUE))
Importance of components:
                       RDA1
                              RDA2 RDA3 RDA4
                                                    RDA5
                                                             RD46
Eigenvalue
                     0.7011 0.5540 0.3660 0.1064 0.03814 0.001279
Proportion Explained 0.3968 0.3135 0.2072 0.0602 0.02159 0.000720
Cumulative Proportion 0.3968 0.7103 0.9175 0.9777 0.99928 1.000000
set.seed(1)
ctrl <- how(nperm = 499,
           within = Within(type = "none").
           plots = with(design, Plots(strata = Stream, type = "free")))
(sig.ws <- anova(m.ws. permutations = ctrl))
Permutation test for rda under reduced model
Plots: Stream, plot permutation: free
Permutation: none
Number of permutations: 499
Model: rda(formula = cravfish ~ Watershed, data = design)
         Df Variance
                          F Pr(>F)
          6 1.7669 21.724 0.002 **
Model
Residual 560 7.5911
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

### HIERARCHICAL ANALYSIS OF CRAYFISH — STREAM SCALE

```
m.str <- rda(crayfish ~ Stream + Condition(Watershed), data = design)</pre>
m.str
Call: rda(formula = cravfish ~ Stream + Condition(Watershed). data
= design)
              Inertia Proportion Rank
Total
             9.3580
                         1.0000
Conditional 1.7669 0.1888
                                   6
Constrained 1.1478 0.1227
                                 10
Unconstrained 6.4433
                     0.6885
                                 10
Inertia is variance
Some constraints were aliased because they were collinear (redundant)
Eigenvalues for constrained axes:
         RDA2
  RDA1
                RDA3
                       RDA4
                              RDA5
                                    RDA6
                                           RDA7
                                                   RDA8
                                                         RDA9
                                                               RDA10
0.4928 0.2990 0.2058 0.0782 0.0372 0.0224 0.0063 0.0030 0.0029 0.0002
Eigenvalues for unconstrained axes:
   PC1
          PC2
                 PC3
                       PC4
                              PC5
                                      PC6
                                            PC7
                                                   PC8
                                                           PC9
                                                                PC10
2.7853 0.8528 0.7737 0.6317 0.5144 0.2808 0.2517 0.1923 0.1559 0.0046
```

### HIERARCHICAL ANALYSIS OF CRAYFISH — STREAM SCALE

Circle ----- 0 1... 1 0 001 1.. 1 0 01 1.1 0 05 1 1 0 1 1 1 1

```
summarv(eigenvals(m.str. constrained = TRUE))
Importance of components:
                                             RD44
                                                     RDA5
                       RDA1
                              RDA2 RDA3
                                                             RDA6
Eigenvalue
                     0.4928 0.2990 0.2058 0.07824 0.03719 0.02235
Proportion Explained 0.4293 0.2605 0.1793 0.06816 0.03240 0.01947
Cumulative Proportion 0.4293 0.6898 0.8691 0.93731 0.96971 0.98918
                         RDA7
                                  RDA8
                                           RDA9
                                                    RDA10
Eigenvalue
                     0.006326 0.003042 0.002894 0.0001546
Proportion Explained 0.005510 0.002650 0.002520 0.0001300
Cumulative Proportion 0.994690 0.997340 0.999870 1.0000000
set.seed(1)
ctrl <- how(nperm = 499.
           within = Within(type = "none").
           plots = with(design, Plots(strata = Reach, type = "free")).
           blocks = with(design, Watershed))
(sig.str <- anova(m.str. permutations = ctrl))
Permutation test for rda under reduced model
Blocks: with(design, Watershed)
Plots: Reach, plot permutation: free
Permutation: none
Number of permutations: 499
Model: rda(formula = cravfish ~ Stream + Condition(Watershed), data = design)
         Df Variance
                          F Pr(>F)
      14 1.1478 6.9477 0.004 **
Lapow
Residual 546 6.4433
```

### HIERARCHICAL ANALYSIS OF CRAYFISH — REACH SCALE

```
m.re <- rda(crayfish ~ Reach + Condition(Stream), data = design)
m.re
Call: rda(formula = cravfish ~ Reach + Condition(Stream), data =
design)
             Inertia Proportion Rank
Total
              9.3580
                       1.0000
Conditional 2.9148
                     0.3115
                                 20
Constrained 1.4829
                     0.1585
                                 10
Unconstrained 4.9603
                      0.5301 10
Inertia is variance
Some constraints were aliased because they were collinear (redundant)
Eigenvalues for constrained axes:
 RDA1
        RDA2
               RDA3
                      RDA4
                             RDA5
                                   RDA6
                                          RDA7
                                                 RDA8
0.6292 0.2706 0.2146 0.1414 0.1123 0.0467 0.0344 0.0270 0.0064 0.0003
Eigenvalues for unconstrained axes:
  PC1
         PC2
                PC3
                       PC4
                              PC5
                                    PC6
                                           PC7
                                                             PC10
                                                  PC8
2.1635 0.6080 0.5605 0.5166 0.3749 0.2212 0.2052 0.1588 0.1477 0.0040
```

### HIERARCHICAL ANALYSIS OF CRAYFISH — REACH SCALE

```
summarv(eigenvals(m.re))
Importance of components:
                         RDA1
                                         RDA3
                                                 RDA4
                                                         RDA5
                                 RDA2
                                                                 RDA6
Eigenvalue
                      0.62923 0.27057 0.21462 0.14135 0.11229 0.04669
Proportion Explained 0.09766 0.04199 0.03331 0.02194 0.01743 0.00725
Cumulative Proportion 0.09766 0.13965 0.17296 0.19490 0.21232 0.21957
                                 RDA8
                                          RDA9
                         RDA7
                                                   RDA10
                                                            PC1
Eigenvalue
                      0.03440 0.02704 0.006381 0.0003486 2.1635 0.60799
Proportion Explained 0.00534 0.00420 0.000990 0.0000500 0.3358 0.09436
Cumulative Proportion 0.22491 0.22911 0.230100 0.2301500 0.5659 0.66029
                          PC3
                                  DC/
                                          PC5
                                                  PC6
Eigenvalue
                      0.56047 0.51656 0.37495 0.22122 0.20516 0.15875
Proportion Explained 0.08699 0.08017 0.05819 0.03433 0.03184 0.02464
Cumulative Proportion 0.74728 0.82745 0.88564 0.91997 0.95181 0.97645
                          PC9
                                  PC10
Eigenvalue
                      0.14770 0.004021
Proportion Explained 0.02292 0.000620
Cumulative Proportion 0.99938 1.000000
set.seed(1)
ctrl <- how(nperm = 499.
            within = Within(type = "none").
            plots = with(design, Plots(strata = Run, type = "free")).
            blocks = with(design, Stream))
(sig.re <- anova(m.re. permutations = ctrl))
```

Permutation test for rda under reduced model Blocks: with(design, Stream) Plots: Run, plot permutation: free

#### HIERARCHICAL ANALYSIS OF CRAYFISH — RUN SCALE

```
m.run <- rda(crayfish ~ Run + Condition(Reach), data = design)
m.run
Call: rda(formula = cravfish ~ Run + Condition(Reach), data =
design)
             Inertia Proportion Rank
Total
              9.3580
                       1.0000
              4.3977 0.4699
Conditional
                                  62
Constrained 1.8225
                     0.1948
                                 10
Unconstrained 3.1378
                      0.3353 10
Inertia is variance
Some constraints were aliased because they were collinear (redundant)
Eigenvalues for constrained axes:
 RDA1
        RDA2
               RDA3
                      RDA4
                             RDA5
                                   RDA6
                                          RDA7
                                                 RDA8
0.8541 0.3141 0.1679 0.1393 0.1328 0.0835 0.0474 0.0429 0.0390 0.0016
Eigenvalues for unconstrained axes:
  PC1
         PC2
                PC3
                       PC4
                              PC5
                                    PC6
                                           PC7
                                                             PC10
                                                  PC8
1.3137 0.4165 0.3832 0.2759 0.2378 0.1725 0.1215 0.1130 0.1016 0.0021
```

### HIERARCHICAL ANALYSIS OF CRAYFISH — RUN SCALE

```
summarv(eigenvals(m.run))
Importance of components:
                        RDA1
                                RDA2
                                        RDA3
                                                RDA4
                                                        RDA5
                                                                RDA6
Eigenvalue
                      0.8541 0.31406 0.16791 0.13925 0.13278 0.08345
Proportion Explained 0.1722 0.06331 0.03385 0.02807 0.02677 0.01682
Cumulative Proportion 0.1722 0.23551 0.26936 0.29743 0.32420 0.34102
                         RDA7
                                 RDA8
                                         RDA9
                                               RDA10
                                                         PC1
Eigenvalue
                     0.04738 0.04289 0.03904 0.00163 1.3137 0.41653
Proportion Explained 0.00955 0.00865 0.00787 0.00033 0.2648 0.08397
Cumulative Proportion 0.35058 0.35922 0.36709 0.36742 0.6323 0.71623
                          PC3
                                  DC/
                                          PC5
                                                  PC6
                                                          DC7
Figenvalue
                     0.38322 0.27587 0.23785 0.17248 0.12150 0.11296
Proportion Explained 0.07726 0.05562 0.04795 0.03477 0.02449 0.02277
Cumulative Proportion 0.79349 0.84910 0.89705 0.93182 0.95632 0.97909
                          PC9
                                  PC10
Eigenvalue
                     0.10158 0.002149
Proportion Explained 0.02048 0.000430
Cumulative Proportion 0.99957 1.000000
set.seed(1)
ctrl <- how(nperm = 499.
           within = Within(type = "free").
           blocks = with(design, Reach))
(sig.run <- anova(m.run, permutations = ctrl))
```

Permutation test for rda under reduced model Blocks: with(design, Reach) Permutation: free Number of permutations: 499



# THE cca.object

- · Objects of class "cca" are complex with many components
- Entire class described in ?cca.object
- $\cdot$  Depending on what analysis performed some components may be NULL
- Used for (C)CA, PCA, RDA, and CAP (capscale())

# THE cca.object

# cca1 has a large number of components

- **\$call** how the function was called
- **\$grand.total** in (C)CA sum of 'rowsum}
- **\$rowsum** the row sums
- **\$colsum** the column sums
- **\$tot.chi** total inertia, sum of Eigenvalues
- **\$pCCA** Conditioned (partial-ed out) components
- **\$CCA** Constrained components
- \$CA Unconstrained components
- **\$method** Ordination method used
- **\$inertia** Description of what inertia is

# THE cca.object

Depending on how one called cca() etc some of these components will be NULL

**\$pCCA** is only filled in if a *partial* constrained ordination fitted

rda() returns objects with classes "rda" and "cca", but in most cases those objects
work like those of class "cca"

The Eigenvalues and axis scores are now spread about the **\$CA** and **\$CCA** components (also **\$pCCA** if a partial CCA)

Thankfully we can use extractor functions to get at such things

# DIAGNOSTICS FOR CONSTRAINED ORDINATIONS | GOODNESS OF FIT

goodness() computes two goodness of fit statistics for species or sites
Which goodness of fit measure is returned is controlled by argument statistic

- statistic = "explained (default) gives the cumulative proportion of variance explained by each axis
- statistic = "distance" gives the residual distance between the "fitted" location in constrained ordination space and the location in the full dimensional space

## DIAGNOSTICS FOR CONSTRAINED ORDINATIONS | GOODNESS OF FIT

## head(goodness(mods))

```
    CCA1
    CCA2
    CCA3

    Callvulg
    0.0062471656
    0.318907619
    0.8254657

    Empenigr
    0.1164701677
    0.137604904
    0.1953245

    Rhodtome
    0.0999089739
    0.169697909
    0.1824153

    Vaccmyrt
    0.2361482843
    0.240516323
    0.2406730

    Vaccviti
    0.1523704591
    0.156502301
    0.2110550

    Pinusylv
    0.0009244423
    0.004802076
    0.0060096
```

```
head(goodness(mods, summarize = TRUE))
```

```
Callvulg Empenigr Rhodtome Vaccmyrt Vaccviti Pinusylv 0.8254657 0.1953245 0.1824153 0.2406730 0.2110550 0.0060096
```

# DIAGNOSTICS FOR CONSTRAINED ORDINATIONS | INERTIA DECOMPOSITION

inertcomp() decomposes the variance in samples or species in partial, constrained, and unconstrained components

Same two types of measure available by argument statistic

- statistic = "explained (default) gives the decomposition in terms of variance
- statistic = "distance" gives decomposition in terms of the the residual distance
- Can output as proportions of total via proportion = TRUE

```
head(inertcomp(mods, proportional = TRUE))
```

```
CCA CA
Callvulg 0.8254657 0.1745343
Empenigr 0.1953245 0.8046755
Rhodtome 0.1824153 0.8175847
Vaccmyrr 0.2406730 0.7593270
Vaccviti 0.2110550 0.7889450
Pinusylv 0.0060096 0.9939904
```

## DIAGNOSTICS FOR CONSTRAINED ORDINATIONS | SPECIES-ENVIRONMENT CORRELATIONS

spenvcor() returns the species-environment correlation

The (weighted) correlation between the weighted average-based and the linear combination-based sets of site scores

A poor measure of goodness of fit. Sensitive to

- outliers (like all correlations)
- overfitting (using too many constraints)

Better models can have poorer species-environment correlations

```
spenvcor(mods)
```

```
CCA1 CCA2 CCA3 0.8554808 0.8132873 0.8792797
```

# DIAGNOSTICS FOR CONSTRAINED ORDINATIONS | INTERSET CORRELATIONS

intersetcor() returns the interset correlations; the (weighted) correlation between
the weighted average-based site scores and each constraint variable

Another poor diagnostic

- correlation based
- focuses on a single constraint–axis combination at a time

Vector fitting (envfit()) or biplot scores (scores(model, display = "bp")) are
better alternatives

```
intersetcor(mods)
```

```
CCA1 CCA2 CCA3
Al 0.7356151 -0.1302334 0.4259623
P -0.3589749 -0.6110772 0.4478933
K -0.3768462 -0.1339192 0.7760441
```

### VARIANCE INFLATION FACTORS

Linear dependencies between constraints can be investigated via the variance inflation factor or VIF

VIF is a measure of how much the variance of  $\hat{\beta}_j$  is inflated by presence of other covariates

Lots of rules of thumb

- VIF >= 20 indicates strong collinearity in constraints
- VIF >= 10 potentially of concern & should be looked at

Computed via vif.cca()

#### **RE-USE**

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### REFERENCES

Blanchet, F Guillaume, Pierre Legendre, and Daniel Borcard. 2008. "Forward Selection of Explanatory Variables." *Ecology* 89 (9). Eco Soc America: 2623–32.