# Epiphyte diversity in a tropical urban habitat

Quantitative Biodiversity 2019

*Diego Rios, Mark Hibbins*

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Our study sought to answer two primary questions: what is the structure of this urban epiphyte community, and how it is affected by the environment, space, and phylogeny? To answer these questions, we first did a cluster analysis of the epiphyte community, and created a cophylogeny of the epiphytes with their host trees, to gain a sense of the broad-scale patterns. Then, we did a phylogenetic distance-based redundancy analysis and a variation partitioning analysis, to statistically test the effects of environment and space on phylogenetic beta-diversity.

## Cluster analysis

To understand overall patterns of epiphyte abundance, we first performed a clustering analysis using the Bray-Curtis distance between sites. First, we setup the workspace:

```
rm(list=ls())
getwd()
```

```
## [1] "/Users/mark/Box Sync/Courses/Quantitative Biodiversity/epiphyte_diversity"
```

```
setwd('/Users/mark/Box Sync/Courses/Quantitative Biodiversity/epiphyte_diversity')

#load packages
package.list <- c('vegan','ade4', 'viridis', 'gplots', 'BiodiversityR', 'indicspecies',
                  'readr')
for (package in package.list) {
  if (!require(package, character.only = TRUE, quietly = TRUE)) {
    install.packages(package)
    library(package, character.only = TRUE)
  }
}
```

```
## This is vegan 2.5-4
```

```
##
## Attaching package: 'gplots'
```

```
## The following object is masked from 'package:stats':
##
##     lowess
```

```
## BiodiversityR 2.11-1: Use command BiodiversityRGUI() to launch the Graphical User Interface;
## to see changes use BiodiversityRGUI(changeLog=TRUE, backward.compatibility.messages=TRUE)
```

```
epiphytes <- read_csv("data/epiphytes.csv") #read in dataset
```

```
## Parsed with column specification:
## cols(
##   .default = col_double(),
##   Phorophyte = col_character()
## )
```

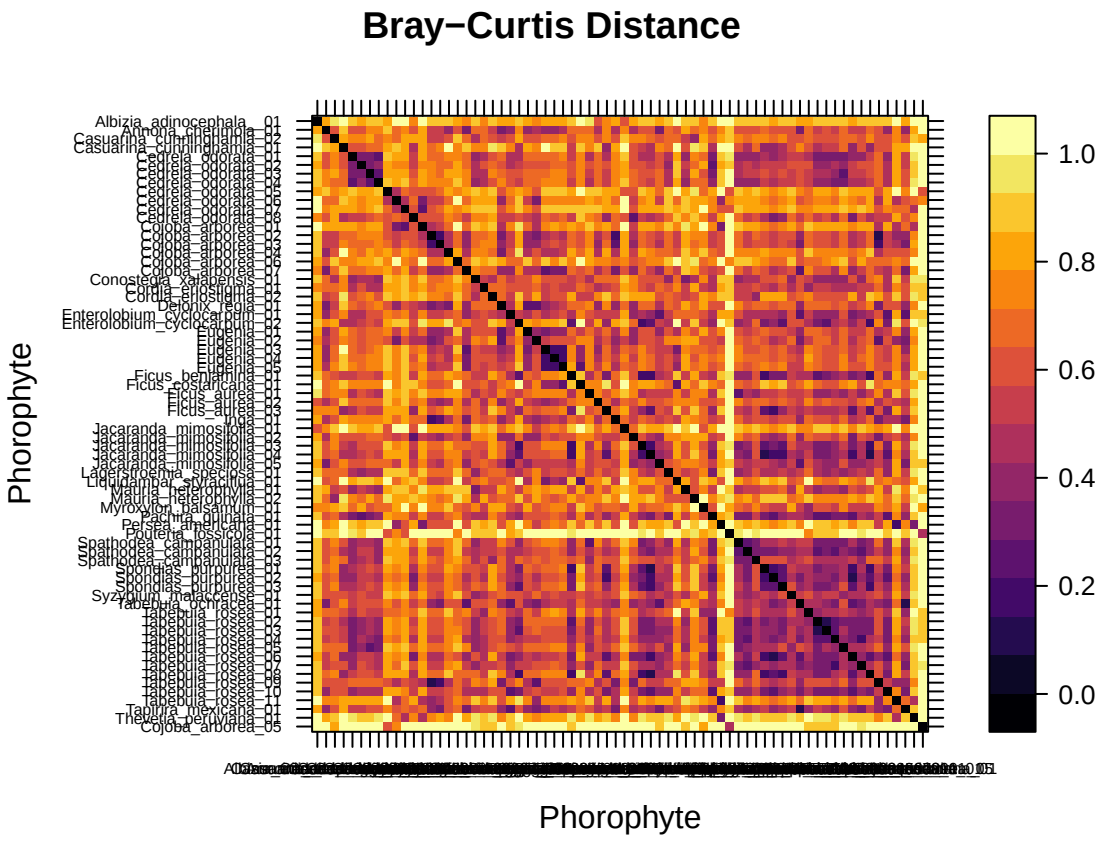
```
## See spec(...) for full column specifications.
```

```
envTrees <- epiphytes[,c(1:6)]
trees <- envTrees[-c(71,72),1]
epiphytes <- epiphytes[-c(71,72),c(-1:-9)]
rownames(epiphytes) <- as.character(trees$Phorophyte)
```

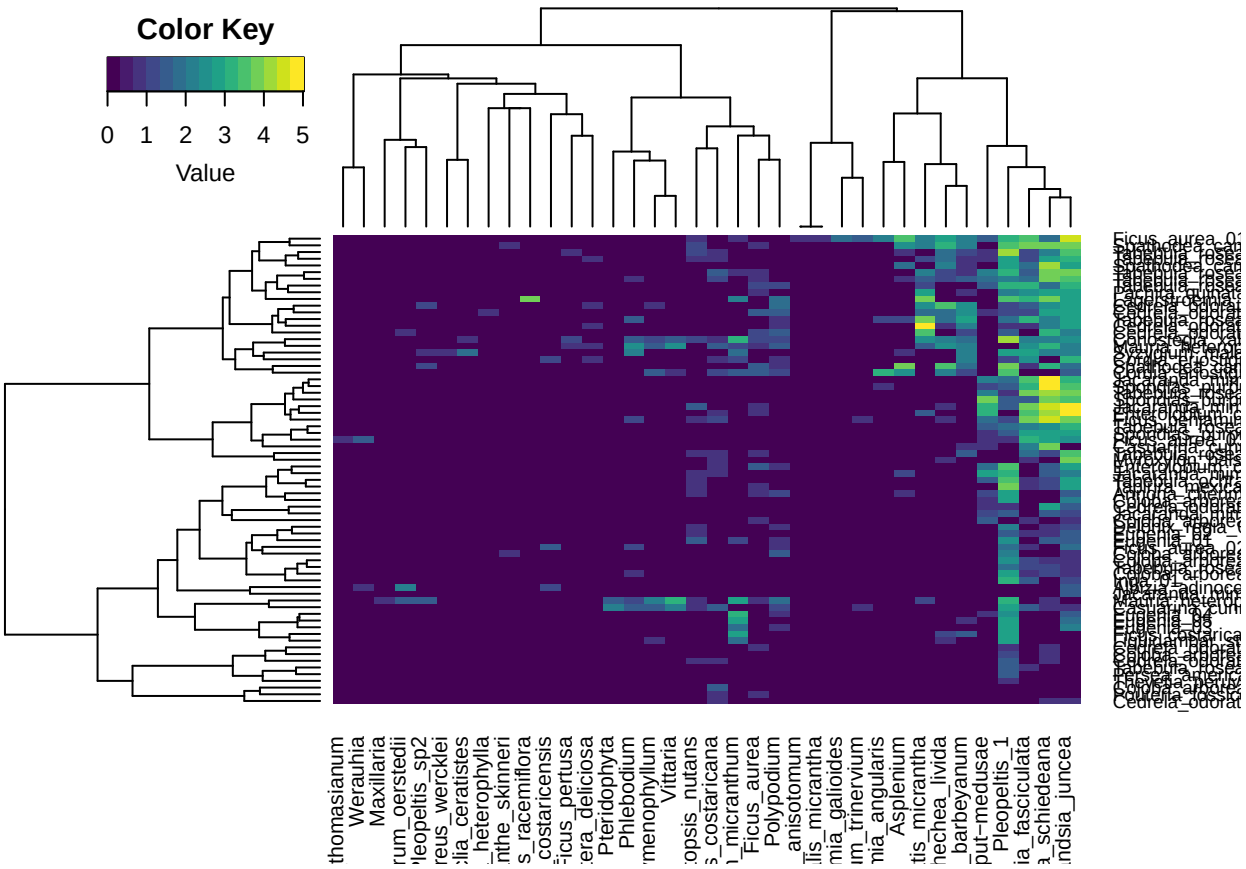
```
## Warning: Setting row names on a tibble is deprecated.
```

Then, we construct a heat map and cluster diagram using the log of epiphyte abundance:

```
epiphytes <- log(1+epiphytes) #log transformation to smooth out values

epiphytes.db <- vegdist(epiphytes, method = "bray", upper = TRUE, diag = TRUE) #distance matrix
order <- rev(attr(epiphytes.db, "Labels")) #Order of labels

#Heat map
levelplot(as.matrix(epiphytes.db)[, order], aspect = "iso",col.regions = inferno,
          xlab = "Phorophyte", ylab = "Phorophyte", scales = list(cex = 0.5),
          main = "Bray-Curtis Distance")
```




```
epiphytes.ward <- hclust(epiphytes.db, method = "ward.D2") #horizontal ward's clustering for the trees

#Cluster diagram
par(mar = c(1,5,2,2)+0.1)
gplots::heatmap.2(as.matrix(epiphytes), distfun = function(x) vegdist(x, method= "bray"),
                  hclustfun = function(x) hclust(x, method = "ward.D2"),
                  col = viridis, trace = "none", density.info="none")
```




These figures reveal some important patterns in our dataset. First, we observe a classic rank-abundance relationship for the epiphytes; a few species are highly abundant, and the majority are relatively rare. Second, the horizontal cluster of trees appears to fall into two major clusters which roughly correspond to deciduousness, ie. whether trees shed their leaves during the dry season. This gives us some initial insights into the factors that may be driving assembly in this community.

## Cophylogeny

One of the interesting properties of our dataset is that each "site" in the site by species matrix corresponds to a taxon of host tree for the epiphytes. Therefore, it is interesting and useful to consider the coevolutionary dynamics between these trees and the epiphytes they host. To this end, we constructed neighbour-joining trees for both groups using sequences from the chloroplast gene maturase K, which is often used for plant DNA barcoding. We then built a cophylogeny to show the co-occurences between trees and epiphytes in a phylogenetic context. First, we load the required packages:

```
package.list <- c('ape', 'seqinr', 'phylobase', 'adephylo', 'geiger', 'picante', 'stats', 'RColorBrewer
                  'caper', 'phylolm', 'pmc', 'ggplot2', 'tidyr', 'dplyr', 'phangorn', 'pander', 'phylos
for (package in package.list) {
  if (!require(package, character.only=TRUE, quietly=TRUE)) {
    install.packages(package)
    library(package, character.only=TRUE)
  }
}
```

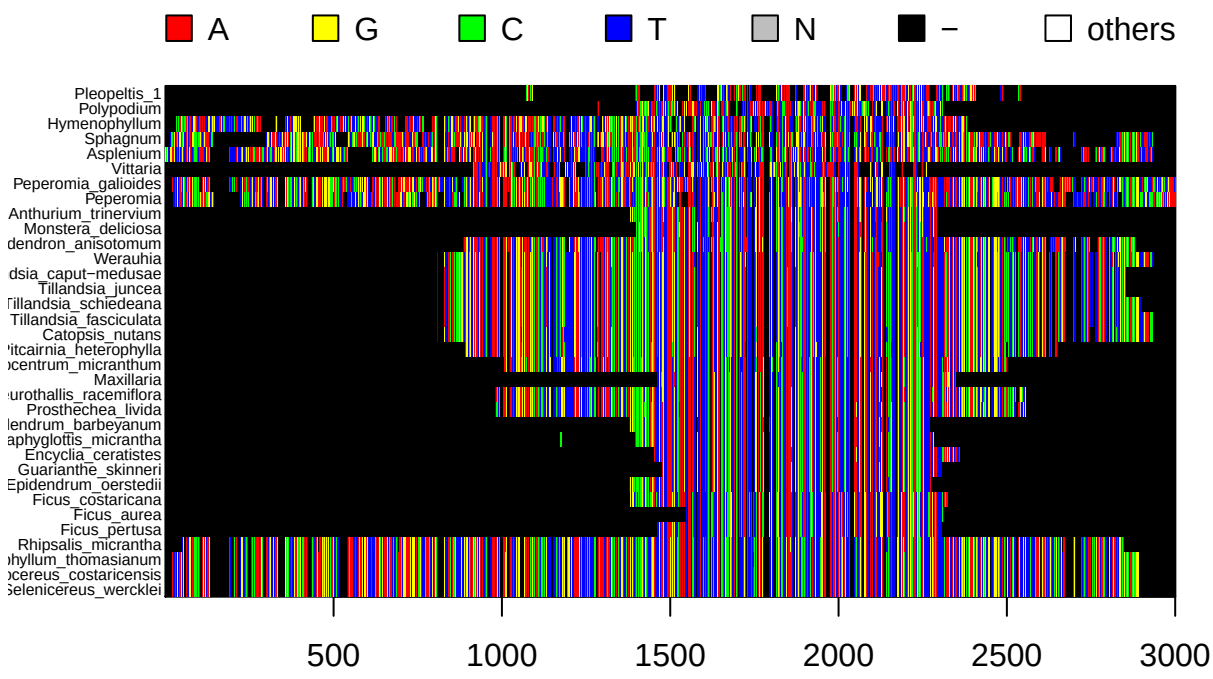
```
##
## Attaching package: 'seqinr'
```

```
## The following objects are masked from 'package:ape':
##
##     as.alignment, consensus
## The following object is masked from 'package:permute':
##
##     getType
##
## Attaching package: 'phylobase'
## The following object is masked from 'package:ape':
##
##     edges
##
## Attaching package: 'nlme'
## The following object is masked from 'package:seqinr':
##
##     gls
##
## Attaching package: 'dplyr'
## The following object is masked from 'package:MASS':
##
##     select
## The following object is masked from 'package:nlme':
##
##     collapse
## The following object is masked from 'package:seqinr':
##
##     count
## The following objects are masked from 'package:stats':
##
##     filter, lag
## The following objects are masked from 'package:base':
##
##     intersect, setdiff, setequal, union
##
## Attaching package: 'phangorn'
## The following objects are masked from 'package:vegan':
##
##     diversity, treedist
## Found more than one class "Annotated" in cache; using the first, from namespace 'RNeXML'
## Also defined by 'S4Vectors'
## Found more than one class "Annotated" in cache; using the first, from namespace 'RNeXML'
## Also defined by 'S4Vectors'
## Found more than one class "Annotated" in cache; using the first, from namespace 'RNeXML'
## Also defined by 'S4Vectors'
```

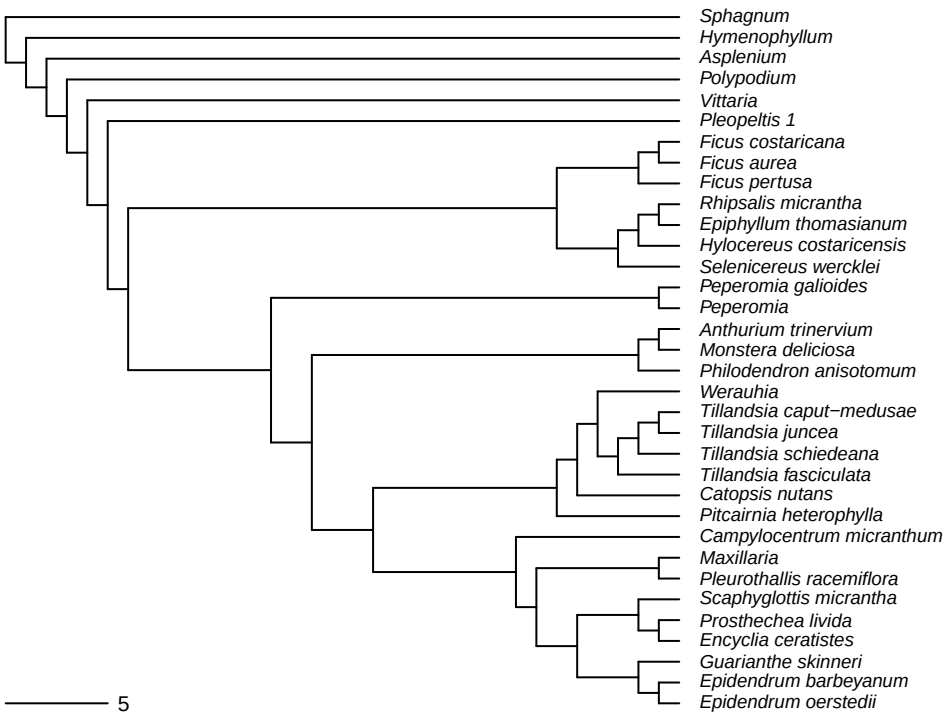
```
## Found more than one class "Annotated" in cache; using the first, from namespace 'RNeXML'
## Also defined by 'S4Vectors'
## Found more than one class "Annotated" in cache; using the first, from namespace 'RNeXML'
## Also defined by 'S4Vectors'
## Found more than one class "Annotated" in cache; using the first, from namespace 'RNeXML'
## Also defined by 'S4Vectors'
```

Next, we read in the alignment files and use them to build neighbour-joining phylogenies. Our alignments were generated using the software 'muscle' with the default parameters.

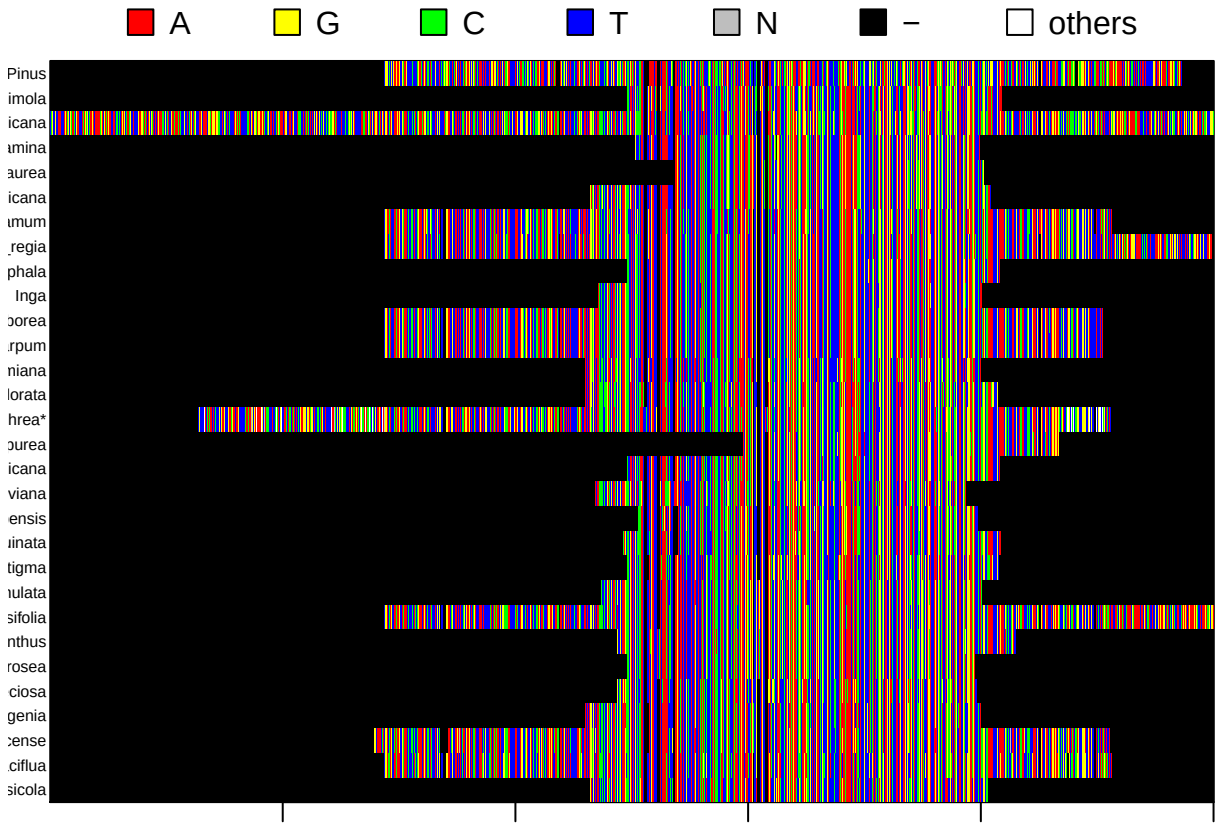
```
ep.aln <- read.alignment(file = './data/epiphytesCRv2_align.fasta', format = 'fasta') #read in alignmen
ep.DNAbin <- as.DNAbin(ep.aln) #convert to DNAbin object
window <- ep.DNAbin[, 0:3000] #pick window to view
image.DNAbin(window, cex.lab = 0.5) #visualize alignment
```



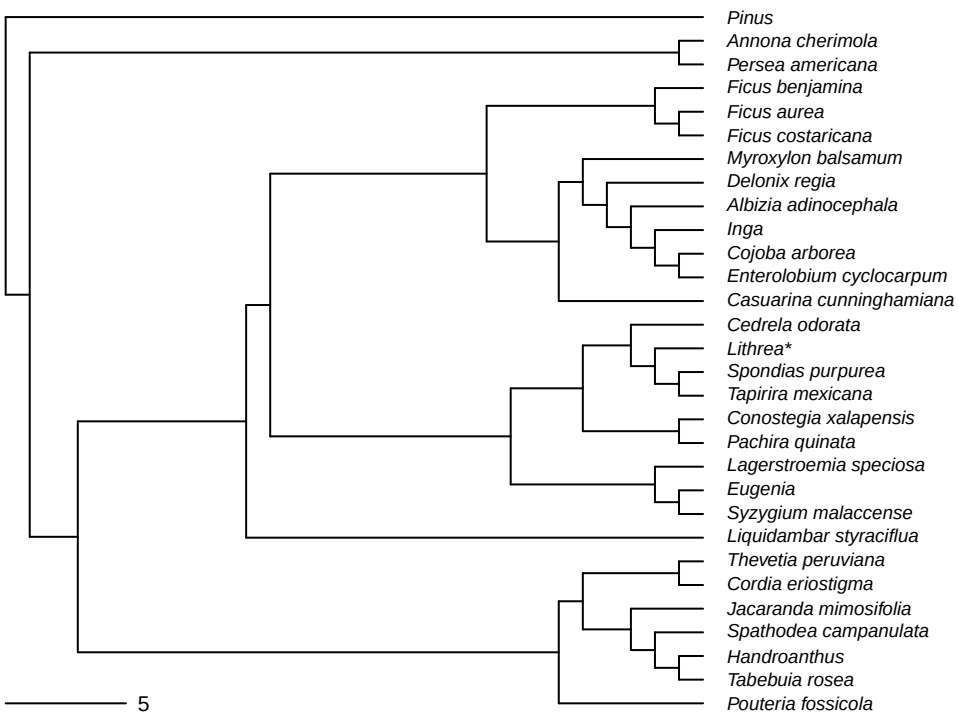

```
ep.dist <- dist.dna(ep.DNAbin[ ,1500:2400], model = 'K80', #make DNA distance matrix using K80 model
                    pairwise.deletion = FALSE, as.matrix = TRUE)
ep.nj.tree <- bionj(ep.dist) #make tree object
outgroup <- match('Sphagnum', ep.nj.tree$tip.label) #define outgroup sequence
ep.nj.tree.rooted <- root(ep.nj.tree, outgroup, resolve.root = TRUE) #root the tree

par(mar = c(1,1,2,1) + 0.1)
plot.phylo(ep.nj.tree.rooted, main = 'Neighbour Joining Tree', 'phylogram',
           use.edge.length = FALSE, direction = 'right',
           cex = 0.6, label.offset = 1)
add.scale.bar(cex = 0.7)
```




```
#Neighbour joining tree for the trees:

tree.aln <- read.alignment(file = './data/trees_align.fasta', format = 'fasta') #read in alignment file
tree.DNAbin <- as.DNAbin(tree.aln) #convert to DNAbin object
window <- tree.DNAbin[, 0:2500] #pick window to view
image.DNAbin(window, cex.lab = 0.5) #visualize alignment
```



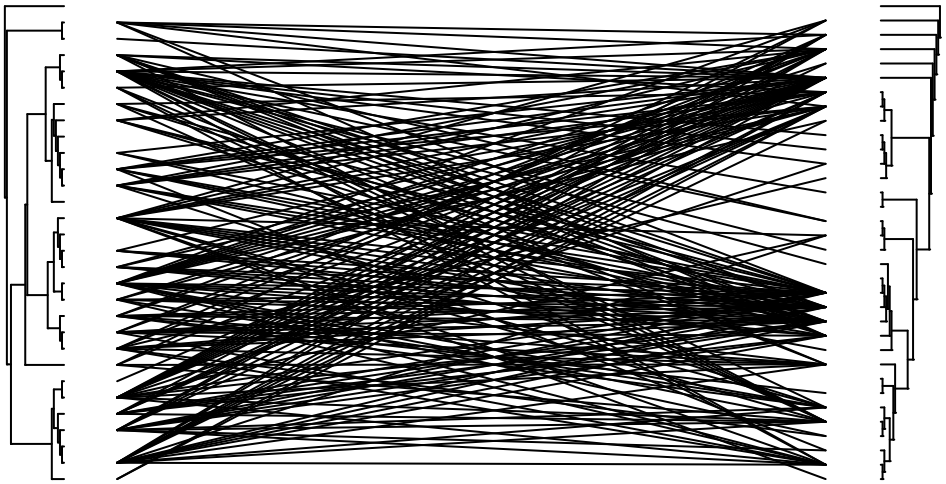

```
tree.dist <- dist.dna(tree.DNAbin[ ,1300:2000], model = 'K80', #make DNA distance matrix using K80 mode
                      pairwise.deletion = FALSE, as.matrix = TRUE)
tree.nj.tree <- bionj(tree.dist) #make tree object
outgroup <- match('Pinus', tree.nj.tree$tip.label) #define outgroup sequence
tree.nj.tree.rooted <- root(tree.nj.tree, outgroup, resolve.root = TRUE) #root the tree

par(mar = c(1,1,2,1) + 0.1)
plot.phylo(tree.nj.tree.rooted, main = 'Neighbour Joining Tree', 'phylogram',
           use.edge.length = FALSE, direction = 'right',
           cex = 0.6, label.offset = 1)
add.scale.bar(cex = 0.7)
```




Finally, we construct a co-ocurrence matrix and use it alongside the phylogenies to build a cophlyogeny:

```
#reload epiphytes data
epiphytes <- read.csv("data/epiphytes.csv")

epiphytes$Phorophyte <- gsub('_([^_]*)$', '', epiphytes$Phorophyte) #cleaning up phorophyte names

trees_cophylo <- vector() #empty vectors for storing co-occurences
epi_cophylo <- vector()

phorophyte_spp <- epiphytes$Phorophyte #list of phorophyte entries

epiphytes <- epiphytes[ ,c(10:45)] #SbyS

epiphytes_spp <- colnames(epiphytes) #list of epiphyte species

for (i in 1:nrow(epiphytes)) {# for each tree entry
  for (j in 1:ncol(epiphytes)) {# for each epiphyte species
    if(epiphytes[i,j] > 0){ #if the epiphyte is present
      if(phorophyte_spp[i] %in% tree.nj.tree.rooted$tip.label) { #check if spp in tree files
        if(epiphytes_spp[j] %in% ep.nj.tree.rooted$tip.label) {
          trees_cophylo <- append(trees_cophylo, phorophyte_spp[i]) #store the tree name
          epi_cophylo <- append(epi_cophylo, epiphytes_spp[j]) #and the epiphyte name
        }
      }
    }
  }
}

cophylo_matrix <- as.data.frame(unique(matrix(c(trees_cophylo,epi_cophylo),
```

```
                                        nrow=371, ncol=2))) #make co-ocurrence matrix

cophyloplot(tree.nj.tree.rooted, ep.nj.tree.rooted, assoc = cophylo_matrix,
            space = 400, length.line = 0, show.tip.label = FALSE)
```



This plot reveals some interesting information about the coevolutionary dynamics between trees (left) and the epiphytes they host (right) (tip labels not shown for clarity). Specifically, it tells us how specialized each epiphyte species is to host trees, and whether this specialization has a phylogenetic signal. For the epiphytes on the right, we can clearly see that the more generalist epiphytes (with many branches coming out of the tips) fall into phylogenetic clusters. One of these clusters, in the bottom half of the tree, contains epiphytes in the genus Tillandsia, which also contain the most abundant species. In constrast, there does not appear to be a strong phylogenetic signal in terms of specialization for the trees in which epiphyte species they prefer to host.

## Phylogenetic distance-based redundancy analysis

Using our phylogenetic data, we can test whether phylogenetic beta diversity is affected by the suite of life history traits we have for both the tree and epiphyte species. Our response matrix for this analysis is abundance-weighted UniFrac distance, as estimated through the `phyloseq` package. First, we need to load in our data and set up the site-by-environment matrix:

```
#epiphyte community data
epiphytes <- read.csv("~/Box Sync/Courses/Quantitative Biodiversity/epiphyte_diversity/data/epiphytes.cs

#epiphyte natural history traits
epiphyte_nat_hist <- read.csv("~/Box Sync/Courses/Quantitative Biodiversity/epiphyte_diversity/data/epi
colnames(epiphyte_nat_hist)[colnames(epiphyte_nat_hist)=='Ornamental'] <- 'ep.ornamental' #rename ornam
epiphyte_nat_hist <- t(epiphyte_nat_hist)[c(1:8), c(2:37)] #transpose and cleanup
colnames(epiphyte_nat_hist) <- as.character(unlist(epiphyte_nat_hist[1,])) #taxa as headers
epiphyte_nat_hist <- epiphyte_nat_hist[c(2:8),] #removed taxa variable

epiphytes_align <- read.alignment(file = './data/epiphytesCRv2_align.fasta',  #epiphytes alignment file
                                  format = 'fasta')

epiphytes_SbyS <- epiphytes[c(1:70), c(8:43)] #epiphyte site-by-species matrix
epiphytes_SbyS <- epiphytes_SbyS[ , order(names(epiphytes_SbyS))] #alphabetical sort by species name

#Missing taxa: Pteridophyta, Phlebodium, Pleopeltis sp 2
```

```
epiphytes_SbyE <- epiphytes[c(1:70), c(2:7)] #First part of site-by-environment matrix
colnames(epiphytes_SbyE)[colnames(epiphytes_SbyE)=='Ornamental'] <- 'tree.ornamental' #rename ornamenta

total_abundances <- rowSums(epiphytes_SbyS) #total epiphyte abundance across sites

for (i in 1:nrow(epiphyte_nat_hist)){ #for each trait
  trait <- t(epiphyte_nat_hist[i,]) #store species values for trait
  traitname <- rownames(epiphyte_nat_hist)[i] #name of trait under consideration
  mean_relative_traits <- vector() #vector to store mean relative trait value for each site

  for (j in 1:nrow(epiphytes_SbyS)){ #for each site in the site by species matrix
    relative_abundances <- epiphytes_SbyS[j,] / total_abundances[j] #relative abundances for the site
    relative_traits <- as.numeric(relative_abundances) * as.numeric(trait) #relativized trait values
    rel_traits <- vector() #vector to store mean relativized trait values

    for (k in 1:length(relative_traits)){ #for each relativized trait value
      if(relative_abundances[k] > 0){ #if the species is present
        rel_traits <- append(rel_traits, relative_traits[k]) #add the relative trait value for the spec
      }
    }
    mean_relative_traits <- append(mean_relative_traits, mean(rel_traits)) #get weighted mean trait val
  }
  epiphytes_SbyE[[traitname]] <- mean_relative_traits #assign traits to columns in site-by-environment
}

epiphytes_SbyE <- scale(epiphytes_SbyE) #normalize (z-normalization) the site-by-environment matrix
```

Now, we can do our phylogenetic dbRDA (which includes model selection):

```
epi_SbyS_otu <- otu_table(epiphytes_SbyS, taxa_are_rows = FALSE) #make otu_table-class object (phyloseq
ep.physeq <- phyloseq(epi_SbyS_otu, ep.nj.tree.rooted) #create physeq object from SbyS + tree
ep.dist.uf <- UniFrac(ep.physeq, weighted = TRUE) #weighted UniFrac distance matrix (phyloseq package)

ep.env.dist <- vegdist(epiphytes_SbyE, method = 'euclid') #environment distance matrix
mantel(ep.dist.uf, ep.env.dist) #Mantel test
```

```
##
## Mantel statistic based on Pearson's product-moment correlation
##
## Call:
## mantel(xdis = ep.dist.uf, ydis = ep.env.dist)
##
## Mantel statistic r: -0.01583
##       Significance: 0.537
##
## Upper quantiles of permutations (null model):
##    90%    95%  97.5%    99%
## 0.0912 0.1186 0.1427 0.1647
## Permutation: free
## Number of permutations: 999
```

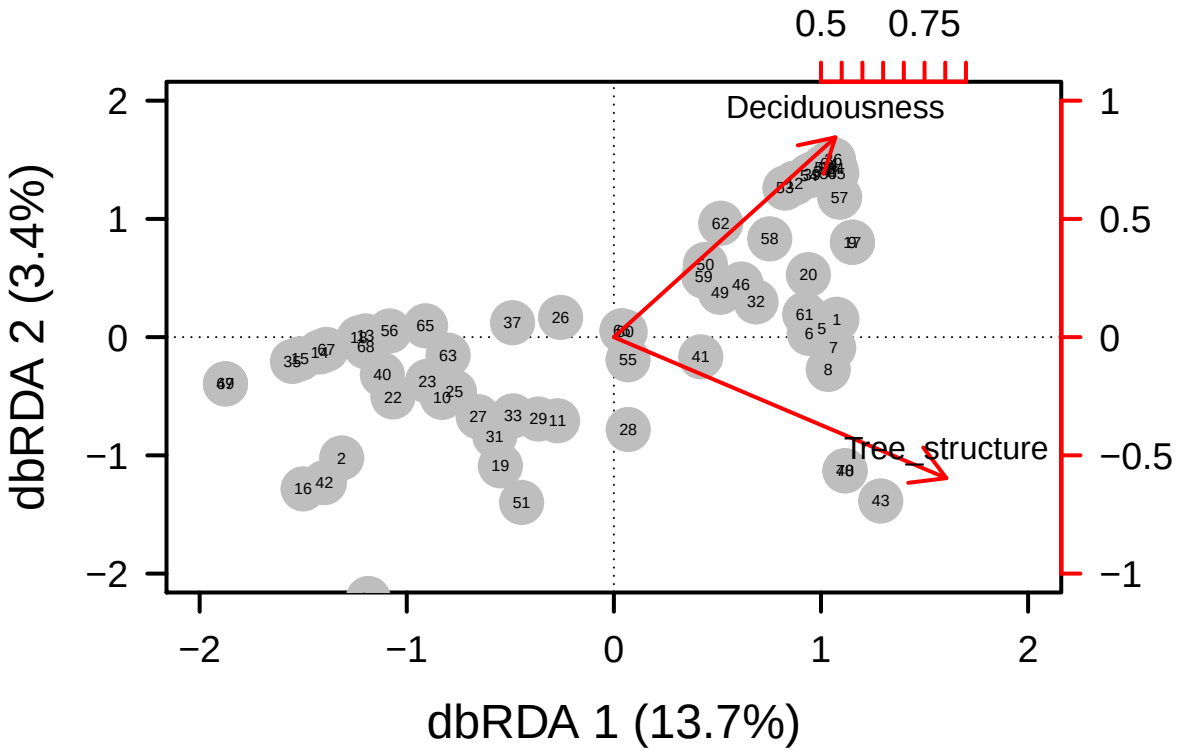
```
epiphytes_phylo_dbrda_int <- vegan::dbrda(ep.dist.uf ~ 1, data = as.data.frame(epiphytes_SbyE)) #interc
epiphytes_phylo_dbrda_full <- vegan::dbrda(ep.dist.uf ~ ., data = as.data.frame(epiphytes_SbyE)) #full
```

```
epiphytes_phylo_dbrda <- ordiR2step(epiphytes_phylo_dbrda_int, epiphytes_phylo_dbrda_full, perm.max = 2
```

```
## Step: R2.adj= 0
## Call: ep.dist.uf ~ 1
##
##                            R2.adjusted
## <All variables>            0.360401765
## + Tree_structure           0.087042299
## + Deciduousness            0.049871511
## + tree.ornamental          0.040218707
## + Rugosity                 0.038505318
## + Wood_density             0.013512723
## <none>                     0.000000000
## + Clonal.growth           -0.005670232
## + Pollination             -0.006544424
## + Photosynthesis          -0.006625487
## + ep.ornamental           -0.006797914
## + Vectorization           -0.007249727
## + Native.Exotic           -0.008835629
## + Habit                   -0.010303819
## + Seed.or.spore.dispersal -0.010788228
##
##                   Df    AIC      F Pr(>F)
## + Tree_structure   1 71.086 7.5785  0.004 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Step: R2.adj= 0.0870423
## Call: ep.dist.uf ~ Tree_structure
##
##                           R2.adjusted
## <All variables>            0.36040176
## + Deciduousness            0.14630169
## + Rugosity                 0.09824852
## + Wood_density             0.09385426
## <none>                     0.08704230
## + tree.ornamental          0.08602525
## + Vectorization            0.08075173
## + Clonal.growth            0.07778514
## + Habit                    0.07758417
## + Seed.or.spore.dispersal  0.07730443
## + Pollination              0.07721296
## + Photosynthesis           0.07718966
## + ep.ornamental            0.07714696
## + Native.Exotic            0.07499226
##
##                  Df    AIC      F Pr(>F)
## + Deciduousness   1 67.351 5.7202  0.006 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Step: R2.adj= 0.1463017
## Call: ep.dist.uf ~ Tree_structure + Deciduousness
##
```

```
##                            R2.adjusted
## <All variables>              0.3604018
## + tree.ornamental            0.1565576
## + Wood_density               0.1511084
## <none>                       0.1463017
## + Habit                      0.1403350
## + Seed.or.spore.dispersal    0.1402117
## + Vectorization              0.1400010
## + Native.Exotic              0.1374391
## + Pollination                0.1357011
## + Photosynthesis             0.1356634
## + Clonal.growth              0.1356196
## + ep.ornamental              0.1355646
## + Rugosity                   0.1340388
##
##                    Df    AIC      F Pr(>F)
## + tree.ornamental   1 67.453 1.8147   0.15
```

```r
ep_dbrda_explainvar1 <- round(epiphytes_phylo_dbrda$CCA$eig[1] / #variation explained on first two axes
                              sum(c(epiphytes_phylo_dbrda$CCA$eig, epiphytes_phylo_dbrda$CA$eig)), 3)
ep_dbrda_explainvar2 <- round(epiphytes_phylo_dbrda$CCA$eig[2] /
                              sum(c(epiphytes_phylo_dbrda$CCA$eig, epiphytes_phylo_dbrda$CA$eig)), 3)

#Plotting the dbrda

par(mar = c(5, 5, 4, 4) + 0.1)

plot(scores(epiphytes_phylo_dbrda, display = 'wa'), xlim = c(-2, 2), ylim = c(-2, 2),
     xlab = paste('dbRDA 1 (', ep_dbrda_explainvar1, '%)', sep = ''),
     ylab = paste('dbRDA 2 (', ep_dbrda_explainvar2, '%)', sep = ''), pch = 16,
     cex = 2.0, type = 'n', cex.lab = 1.5, cex.axis = 1.2, axes = FALSE
     )

axis(side = 1, labels = T, lwd.ticks = 2, cex.axis = 1.2, las = 1)
axis(side = 2, labels = T, lwd.ticks = 2, cex.axis = 1.2, las = 1)
abline(h = 0, v = 0, lty = 3)
box(lwd = 2)

points(scores(epiphytes_phylo_dbrda, display = 'wa'),
       pch = 19, cex = 3, bg = 'gray', col = 'gray')
text(scores(epiphytes_phylo_dbrda, display = 'wa'),
     labels = row.names(scores(epiphytes_phylo_dbrda, display = 'wa')), cex = 0.5)

vectors <- scores(epiphytes_phylo_dbrda, display = 'bp')

arrows(0, 0, vectors[,1] * 2, vectors[, 2] * 2,
       lwd = 2, lty = 1, length = 0.2, col = "red")
text(vectors[,1] * 2, vectors[, 2] * 2, pos = 3,
     labels = row.names(vectors))
axis(side = 3, lwd.ticks = 2, cex.axis = 1.2, las = 1, col = "red", lwd = 2.2,
     at = pretty(range(vectors[, 1])) * 2, labels = pretty(range(vectors[, 1])))
axis(side = 4, lwd.ticks = 2, cex.axis = 1.2, las = 1, col = "red", lwd = 2.2,
     at = pretty(range(vectors[, 2])) * 2, labels = pretty(range(vectors[, 2])))
```




The best model for phylogenetic beta diversity contains only two predictors, both of which are characteristics of the host tree species: deciduousness and tree structure. Seeing deciduousness in this model is consistent with the broad groupings we saw in our cluster diagram, and it also makes sense biologically, since the presence or absence of leaves during certain parts of the year affects the microclimate of the host tree. The other variable, tree structure, is a compound variable that can encapsulate many factors, including the age of the tree and the kinds of spatial niches that may be available for epiphytes to grow.

It is somewhat surprising that none of the epiphyte life history traits turned up as important in the final model. The reasonable interpretation of this seems to be that they are tightly correlated to tree traits, rather than being unimportant in structuring epiphyte communities.

## Variation partitioning

Our final analysis was variation partitioning of phylogenetic beta diversity into environmental and spatial components. This analysis gives us some idea of how our life history traits interact with space to affect the epiphyte community.

```
#Space
ep.x <- epiphytes[-c(71,72),8]/min(epiphytes[-c(71,72),8])
ep.y <- epiphytes[-c(71,72),9]/max(epiphytes[-c(71,72),9])
ep.xy <- cbind(ep.x,ep.y)

ep.coords <- pcnm(dist(ep.xy), dist.ret = T)
ep.coords$values > 0
```

```
##  [1]  TRUE  TRUE  TRUE  TRUE  TRUE  TRUE  TRUE  TRUE  TRUE  TRUE  TRUE
## [12]  TRUE  TRUE  TRUE  TRUE  TRUE  TRUE  TRUE  TRUE  TRUE  TRUE FALSE
## [23] FALSE FALSE FALSE FALSE FALSE FALSE FALSE FALSE FALSE FALSE FALSE
## [34] FALSE FALSE FALSE
```

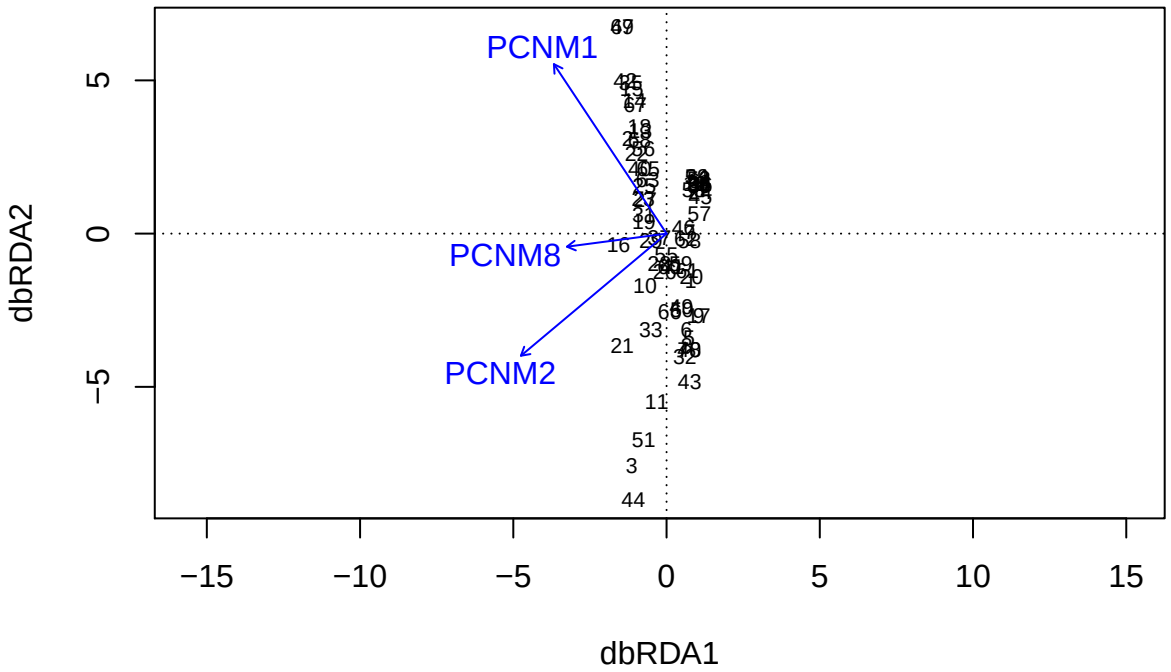
```r
ep.space <- as.data.frame(scores(ep.coords))
ep.pcnm.mod0 <- dbrda(ep.dist.uf ~ 1, ep.space)
ep.pcnm.mod1 <- dbrda(ep.dist.uf ~ ., ep.space)
step.pcnm <- ordiR2step(ep.pcnm.mod0, ep.pcnm.mod1, perm.max = 200)
```

```
## Step: R2.adj= 0
## Call: ep.dist.uf ~ 1
##
##                   R2.adjusted
## <All variables>  0.2170108589
## + PCNM2          0.0714079384
## + PCNM1          0.0385029919
## + PCNM8          0.0257156734
## + PCNM11         0.0233339042
## + PCNM21         0.0220069087
## + PCNM7          0.0152970116
## + PCNM3          0.0128720254
## + PCNM12         0.0041831778
## + PCNM20         0.0024179302
## + PCNM5          0.0022573580
## + PCNM18         0.0017208436
## <none>           0.0000000000
## + PCNM4         -0.0001544099
## + PCNM9         -0.0015007261
## + PCNM15        -0.0038669515
## + PCNM17        -0.0041937034
## + PCNM14        -0.0064579248
## + PCNM16        -0.0071156863
## + PCNM6         -0.0096190151
## + PCNM13        -0.0104464015
## + PCNM10        -0.0111797197
## + PCNM19        -0.0119970892
##
##         Df    AIC     F Pr(>F)
## + PCNM2  1 72.275 6.306  0.006 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Step: R2.adj= 0.07140794
## Call: ep.dist.uf ~ PCNM2
##
##                  R2.adjusted
## <All variables>  0.21701086
## + PCNM1          0.11155139
## + PCNM8          0.09857322
## + PCNM11         0.09615590
## + PCNM21         0.09480910
## + PCNM7          0.08799905
## + PCNM3          0.08553787
## + PCNM12         0.07671934
## + PCNM20         0.07492775
## + PCNM5          0.07476478
## + PCNM18         0.07422026
## + PCNM4          0.07231701
```

```
## <none>           0.07140794
## + PCNM9          0.07095060
## + PCNM15         0.06854906
## + PCNM17         0.06821743
## + PCNM14         0.06591942
## + PCNM16         0.06525184
## + PCNM6          0.06271115
## + PCNM13         0.06187141
## + PCNM10         0.06112715
## + PCNM19         0.06029758
##
##         Df    AIC      F Pr(>F)
## + PCNM1  1 70.144 4.0725   0.02 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Step: R2.adj= 0.1115514
## Call: ep.dist.uf ~ PCNM2 + PCNM1
##
##                 R2.adjusted
## <All variables>   0.2170109
## + PCNM8           0.1397365
## + PCNM11          0.1372826
## + PCNM21          0.1359153
## + PCNM7           0.1290021
## + PCNM3           0.1265037
## + PCNM12          0.1175515
## + PCNM20          0.1157328
## + PCNM5           0.1155673
## + PCNM18          0.1150146
## + PCNM4           0.1130825
## + PCNM9           0.1116954
## <none>            0.1115514
## + PCNM15          0.1092574
## + PCNM17          0.1089208
## + PCNM14          0.1065879
## + PCNM16          0.1059103
## + PCNM6           0.1033311
## + PCNM13          0.1024786
## + PCNM10          0.1017231
## + PCNM19          0.1008809
##
##         Df    AIC      F Pr(>F)
## + PCNM8  1 68.835 3.1951  0.032 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Step: R2.adj= 0.1397365
## Call: ep.dist.uf ~ PCNM2 + PCNM1 + PCNM8
##
##                 R2.adjusted
## <All variables>   0.2170109
## + PCNM11          0.1662971
## + PCNM21          0.1649089
```

```
## + PCNM7           0.1578893
## + PCNM3           0.1553524
## + PCNM12          0.1462625
## + PCNM20          0.1444158
## + PCNM5           0.1442478
## + PCNM18          0.1436866
## + PCNM4           0.1417248
## + PCNM9           0.1403163
## <none>            0.1397365
## + PCNM15          0.1378409
## + PCNM17          0.1374990
## + PCNM14          0.1351303
## + PCNM16          0.1344422
## + PCNM6           0.1318233
## + PCNM13          0.1309578
## + PCNM10          0.1301906
## + PCNM19          0.1293355
##
##          Df    AIC      F Pr(>F)
## + PCNM11  1 67.571 3.1027  0.056 .
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
plot(step.pcnm)
```




```
step.pcnm$anova
```

```
##                   R2.adj Df    AIC      F Pr(>F)
## + PCNM2         0.071408  1 72.275 6.3060  0.006 **
## + PCNM1         0.111551  1 70.144 4.0725  0.020 *
## + PCNM8         0.139737  1 68.835 3.1951  0.032 *
## <All variables> 0.217011
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
space.mod <- model.matrix(~ PCNM2 + PCNM1 + PCNM8, ep.space)[,-1]
env.mod <- model.matrix(~ Tree_structure + Deciduousness, as.data.frame(epiphytes_SbyE))[,-1]

ep.total.env <- dbrda(ep.dist.uf ~ env.mod)
ep.total.space <- dbrda(ep.dist.uf ~ space.mod)

#partial constrained ordinations
ep.env.cond.space <- dbrda(ep.dist.uf ~ env.mod + Condition(space.mod))
ep.space.cond.space <- dbrda(ep.dist.uf ~ space.mod + Condition(env.mod))

#significance
permutest(ep.env.cond.space, permutations = 999)
```

```
##
## Permutation test for dbrda under reduced model
##
## Permutation: free
## Number of permutations: 999
##
## Model: dbrda(formula = ep.dist.uf ~ env.mod +
## Condition(space.mod))
## Permutation test for all constrained eigenvalues
##          Df Inertia      F Pr(>F)
## Model     2 0.49201 8.1694  0.001 ***
## Residual 64 1.92725
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
permutest(ep.space.cond.space, permutations = 999)
```

```
##
## Permutation test for dbrda under reduced model
##
## Permutation: free
## Number of permutations: 999
##
## Model: dbrda(formula = ep.dist.uf ~ space.mod +
## Condition(env.mod))
## Permutation test for all constrained eigenvalues
##          Df Inertia      F Pr(>F)
## Model     3 0.50992 5.6445  0.001 ***
## Residual 64 1.92725
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
permutest(ep.total.env, permutations = 999)
```

```
##
## Permutation test for dbrda under reduced model
##
## Permutation: free
## Number of permutations: 999
##
## Model: dbrda(formula = ep.dist.uf ~ env.mod)
## Permutation test for all constrained eigenvalues
```

```
##          Df Inertia      F Pr(>F)
## Model     2 0.50289 6.9124  0.001 ***
## Residual 67 2.43717
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
permutest(ep.total.space, permutations = 999)
```

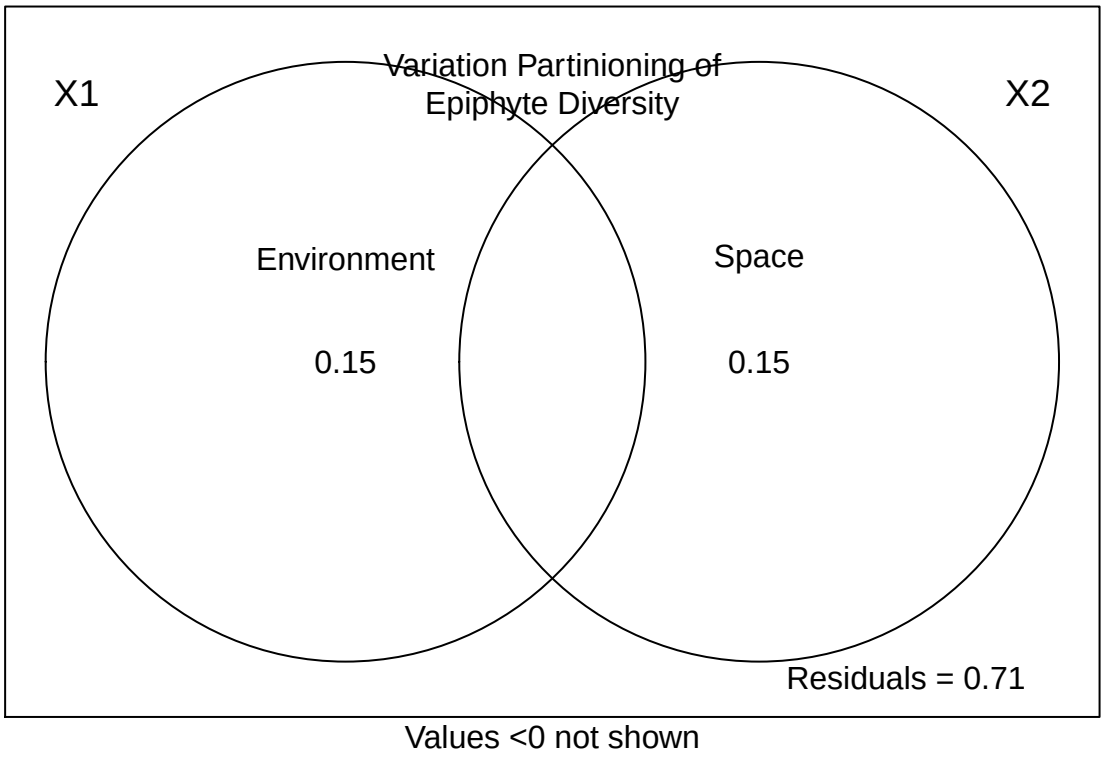
```
##
## Permutation test for dbrda under reduced model
##
## Permutation: free
## Number of permutations: 999
##
## Model: dbrda(formula = ep.dist.uf ~ space.mod)
## Permutation test for all constrained eigenvalues
##          Df Inertia     F Pr(>F)
## Model     3  0.5208 4.736  0.001 ***
## Residual 66  2.4193
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
ep.varpart <- varpart(ep.dist.uf, env.mod, space.mod)


ep.varpart
```

```
##
## Partition of squared  distance in dbRDA
##
## Call: varpart(Y = ep.dist.uf, X = env.mod, space.mod)
##
## Explanatory tables:
## X1:  env.mod
## X2:  space.mod
##
## No. of explanatory tables: 2
## Total variation (SS): 2.9401
## No. of observations: 70
##
## Partition table:
##                       Df R.squared Adj.R.squared Testable
## [a+b] = X1             2   0.17105       0.14630     TRUE
## [b+c] = X2             3   0.17714       0.13974     TRUE
## [a+b+c] = X1+X2        5   0.34449       0.29327     TRUE
## Individual fractions
## [a] = X1|X2            2                 0.15354     TRUE
## [b]                    0                -0.00724    FALSE
## [c] = X2|X1            3                 0.14697     TRUE
## [d] = Residuals                          0.70673    FALSE
## ---
## Use function 'dbrda' to test significance of fractions of interest
```

```
par(mar = c(2,2,2,2))
plot(ep.varpart)
text(1, 0.25, "Space")
```

```
text(0, 0.25, "Environment")
mtext("Variation Partinioning of\nEpiphyte Diversity", side = 3, line = -3)
```




```
#dev.off()
```

The results of this analysis suggest that 1) the individual effects of environment and space are about equally important; 2) there is no variation explained by the covariance of environment and space. The second finding is somewhat surprising, since we might expect environmental variables to vary over space. However, our dataset is unique in that our environmental variables are all biotic, and may not vary with space in a predictable manner like abiotic factors would. It is also possible that our study site is too small for environment-space relationships to manifest, although this seems unlikely.