

# Genotypic variation in a foundation tree species contributes to arthropod interaction network structure



## Abstract

- Multiple studies have demonstrated that genetic variation in a single species can structure entire communities and tri-trophic interactions; however, few studies have examined evolutionary dynamics in complex ecological networks.
- Here, we use a long-term experimental common garden to test for the effect that genotypic variation in a foundation species (*Populus angustifolia* James) in its interactions with a common insect (*Pemphigus betae*) can affect a larger community network of arthropods.
- While other studies have shown such effects on community richness, abundance and composition, this study aims to determine the impact of genotypic variation on networks of interactions in multi-species, complex communities.
- Three main results emerged:
  1. Tree genotype significantly impacted the similarity of arthropod interaction network by re-wiring network.
  2. Leaf senescence, a genetically based trait, also contributed to interaction network similarity and had a marginal effect on network centrality.
  3. Genetically based resistance to *P. betae*, also played a major role to a more diverse group of leaf chewing insects, including a gall boring insect that attacks *P. betae*.
- The results suggest that tree genotype can influence the structure of associated arthropod interaction networks and demonstrate how genetic variance in foundation plant species can affect the structure of ecological networks through its interactions with a common herbivore, which adds further support to the interacting foundation species hypothesis in which the genetics-based interactions of a few highly interactive species can define whole communities of organisms. Together, these findings demonstrate

how community-level genetic effects contribute to ecological patterns and provide a potential mechanism for evolutionary dynamics in complex ecosystems.

Weighted and probabilistic analyses:

```
### load pit data
source('../src/loadPitdata.R')

head(summary(tree.info))
```

```
## leaf.type      tree      geno      leaves
## "live:36 " "np12.04: 2 " "1000 :12 " "Min. : 0.00 "
## "sen :36 " "np12.07: 2 " "1008 :10 " "1st Qu.: 38.75 "
## NA      "np13.10: 2 " "1017 :10 " "Median : 50.00 "
## NA      "np2.07 : 2 " "1023 :10 " "Mean : 61.26 "
## NA      "np2.08 : 2 " "11 :10 " "3rd Qu.: 50.00 "
## NA      "np2.10 : 2 " "996 :10 " "Max. :464.00 "
```

```
head(summary(tree.arth))
```

```
##           Length Class      Mode
## live np12.04 1017 "16" "data.frame" "list"
## live np12.07 1017 "16" "data.frame" "list"
## live np13.10 1017 "16" "data.frame" "list"
## live np2.07 1000 "16" "data.frame" "list"
## live np2.08 996  "16" "data.frame" "list"
## live np2.10 996  "16" "data.frame" "list"
```

```
head(summary(arth.mats))
```

```
##           Length Class      Mode
## live np12.04 1017 "800" "-none-" "numeric"
## live np12.07 1017 "800" "-none-" "numeric"
## live np13.10 1017 "800" "-none-" "numeric"
## live np2.07 1000 "800" "-none-" "numeric"
## live np2.08 996  "800" "-none-" "numeric"
## live np2.10 996  "800" "-none-" "numeric"
```

Generate the network using the co-occurrences of each arthropod on a leaf.

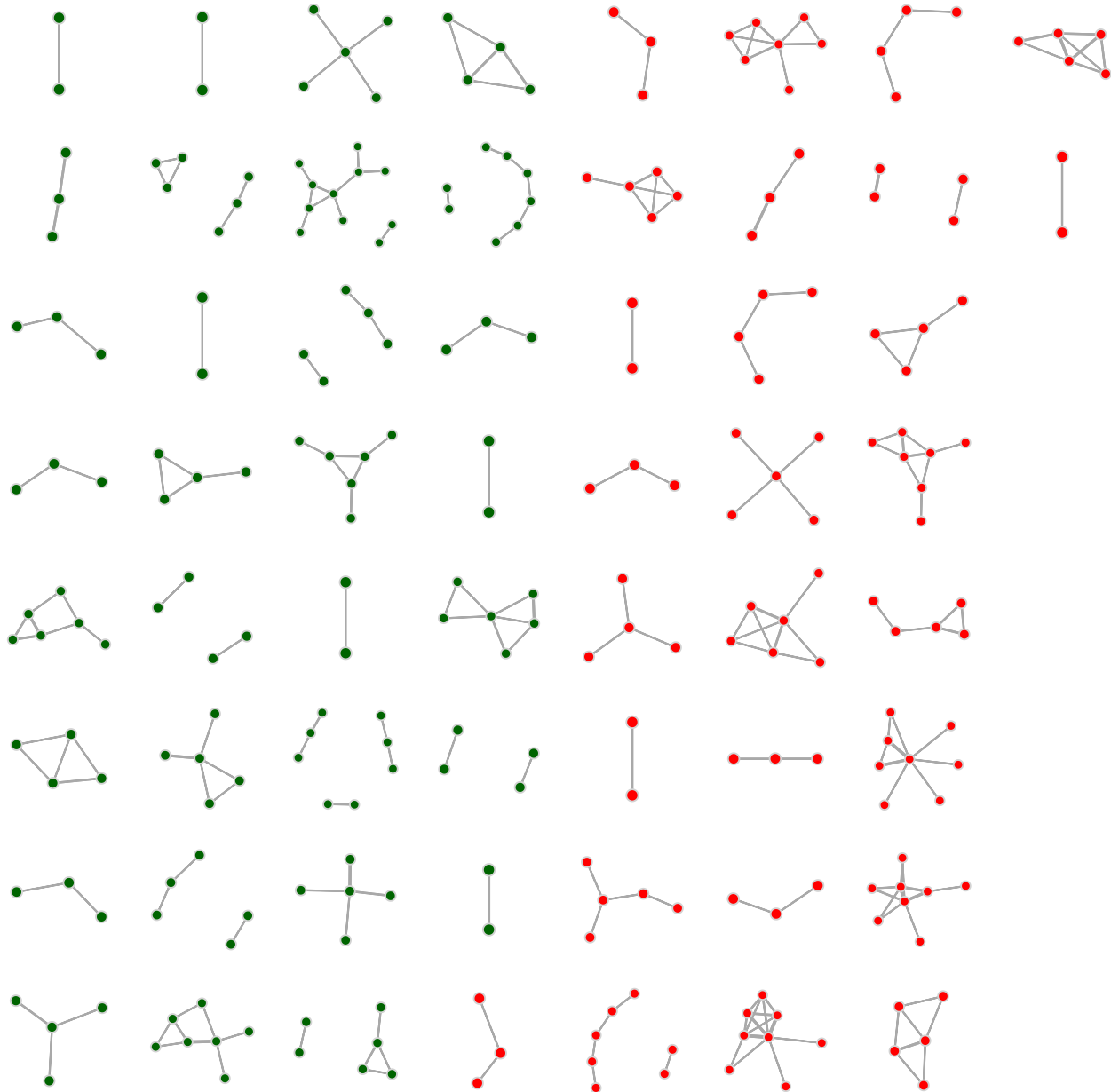
```
library(sna)
nets.plot <- lapply(tree.nets,rmZeros)

par(mfcol=c(8,9),mai=rep(0.1,4))
for (i in 1:length(nets.plot)){
  if (sum(dim(nets.plot[[i]])) != 0){
    if (tree.info[i,1] == 'sen'){
      vc <- 'red'
    }else{vc <- 'darkgreen'}
    gplot(nets.plot[[i]],gmode='graph',
          edge.col='darkgrey',vertex.col=vc,
```

```

    vertex.border='lightgrey',
    edge.lwd=nets.plot[[i]],vertex.cex=2)
  }
}

```



```
t.test(I(liv.evc-sen.evc))
```

```

##
## One Sample t-test
##
## data: I(liv.evc - sen.evc)
## t = 1.4193, df = 23, p-value = 0.1692
## alternative hypothesis: true mean is not equal to 0

```

```
## 95 percent confidence interval:
## -0.01546495 0.08306690
## sample estimates:
## mean of x
## 0.03380098
```

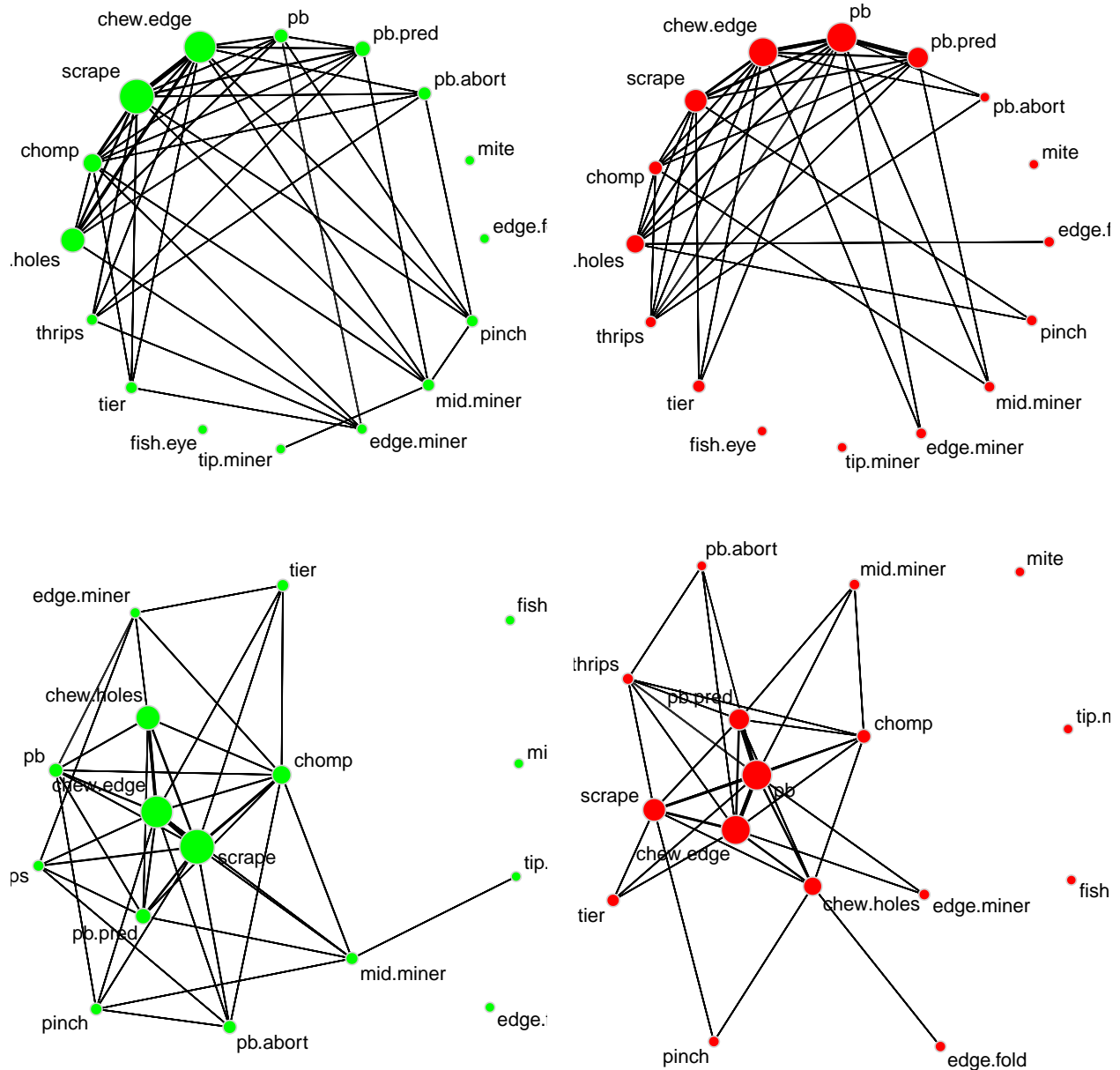
```
t.test(I(liv.dc-sen.dc))
```

```
##
## One Sample t-test
##
## data: I(liv.dc - sen.dc)
## t = -1.3324, df = 35, p-value = 0.1914
## alternative hypothesis: true mean is not equal to 0
## 95 percent confidence interval:
## -0.22098995 0.04585768
## sample estimates:
## mean of x
## -0.08756614
```

Analyze the mean networks for live and senescent leaves.

```
# average structure and variance
liv.mu <- meanNet(liv.nets)
liv.var <- varNet(liv.nets)
sen.mu <- meanNet(sen.nets)
sen.var <- varNet(sen.nets)

par(mfrow=c(2,2),mai=rep(0.1,4))
gplot(liv.mu,gmode='graph',
      edge.lwd=liv.mu/max(liv.mu)*3,vertex.col='green',
      vertex.border='lightgrey',
      edge.col=grey(liv.var/max(liv.var)),
      vertex.cex=apply(liv.spc,2,mean) * 3 + 0.5,
      mode='circle',displaylabels=TRUE)
gplot(sen.mu,gmode='graph',
      edge.lwd=sen.mu/max(sen.mu)*3,vertex.col='red',
      vertex.border='lightgrey',
      edge.col=grey(sen.var/max(sen.var)),
      vertex.cex=apply(sen.spc,2,mean) * 3 + 0.5,
      mode='circle',displaylabels=TRUE)
gplot(liv.mu,gmode='graph',
      edge.lwd=liv.mu/max(liv.mu)*3,vertex.col='green',
      vertex.border='lightgrey',
      edge.col=grey(liv.var/max(liv.var)),
      vertex.cex=apply(liv.spc,2,mean) * 3 + 0.5,
      displaylabels=TRUE)
gplot(sen.mu,gmode='graph',
      edge.lwd=sen.mu/max(sen.mu)*3,vertex.col='red',
      vertex.border='lightgrey',
      edge.col=grey(sen.var/max(sen.var)),
      vertex.cex=apply(sen.spc,2,mean) * 3 + 0.5,
      displaylabels=TRUE)
```



Number of senescing leaves influences the order but not the centrality (eigen) of the networks or the network similarity of senescing leaves.

```
n.lfs <- tree.info$leaves[tree.info$leaf.type == 'sen']
cor.test(n.lfs, I(liv.dc-sen.dc))
```

```
##
## Pearson's product-moment correlation
##
## data:  n.lfs and I(liv.dc - sen.dc)
## t = -1.5167, df = 34, p-value = 0.1386
## alternative hypothesis: true correlation is not equal to 0
## 95 percent confidence interval:
##  -0.53594682  0.08372385
## sample estimates:
```

```
##          cor
## -0.2517362
```

```
cor.test(n.lfs,I(liv.evc-sen.evc))
```

```
##
## Pearson's product-moment correlation
##
## data:  n.lfs and I(liv.evc - sen.evc)
## t = 0.52122, df = 22, p-value = 0.6074
## alternative hypothesis: true correlation is not equal to 0
## 95 percent confidence interval:
## -0.3066130  0.4919243
## sample estimates:
##          cor
## 0.1104442
```

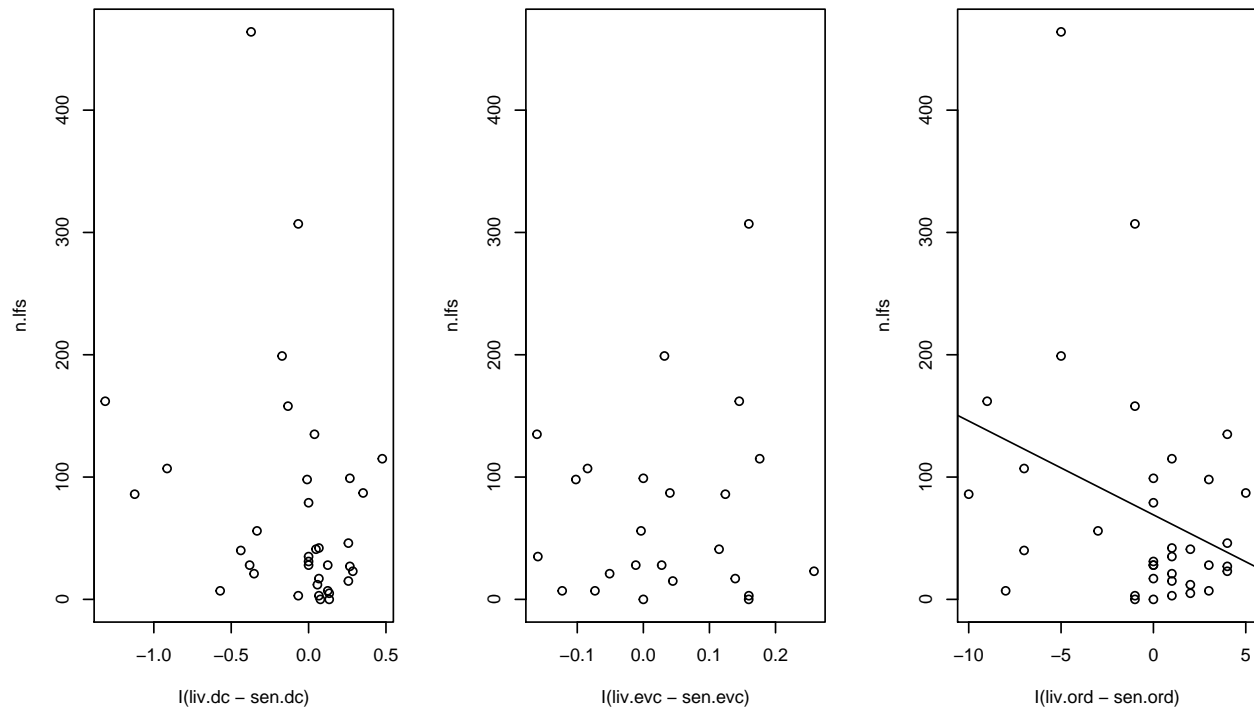
```
cor.test(n.lfs,I(liv.ord-sen.ord))
```

```
##
## Pearson's product-moment correlation
##
## data:  n.lfs and I(liv.ord - sen.ord)
## t = -1.9501, df = 34, p-value = 0.05945
## alternative hypothesis: true correlation is not equal to 0
## 95 percent confidence interval:
## -0.5847730  0.0126857
## sample estimates:
##          cor
## -0.3171719
```

```
adonis(distNet(tree.nets[tree.info$leaf.type == 'sen'])~n.lfs)
```

```
##
## Call:
## adonis(formula = distNet(tree.nets[tree.info$leaf.type == "sen"]) ~      n.lfs)
##
## Permutation: free
## Number of permutations: 999
##
## Terms added sequentially (first to last)
##
##          Df SumsOfSqs MeanSqs F.Model      R2 Pr(>F)
## n.lfs      1      37.85  37.849  1.3597 0.03845  0.198
## Residuals 34     946.43  27.836      0.96155
## Total     35     984.28      1.00000
```

```
par(mfrow=c(1,3))
plot(I(liv.dc-sen.dc),n.lfs)
plot(I(liv.evc-sen.evc),n.lfs)
plot(I(liv.ord-sen.ord),n.lfs)
abline(lm(n.lfs~I(liv.ord-sen.ord)))
```



How much variance in network structure does genotype explain?

About 8% of the variation in network structure was attributable to tree genotype. This was primarily due to genetic effects on re-wiring of the network rather than changes to the structure.

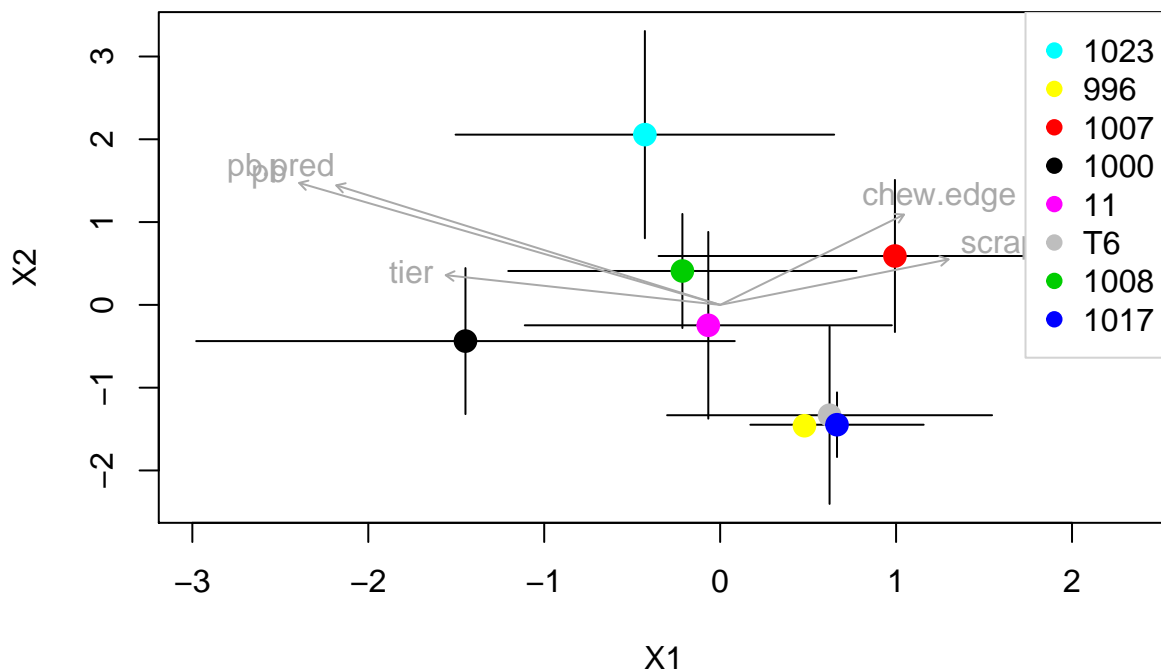
```
library(BiodiversityR)
library(ecodist)
dn.tree <- distNet(tree.nets)
adonis(dn.tree~factor(leaf.type)*factor(geno),data=tree.info, strata=tree.info$tree)
```

```
##
## Call:
## adonis(formula = dn.tree ~ factor(leaf.type) * factor(geno),      data = tree.info, strata = tree.in
##
## Blocks: strata
## Permutation: free
## Number of permutations: 999
##
## Terms added sequentially (first to last)
##
##              Df SumsOfSqs MeanSqs F.Model    R2 Pr(>F)
## factor(leaf.type)      1    118.53  118.528  5.3315 0.07390 0.001
## factor(geno)           7     123.52   17.646  0.7937 0.07702 0.005
## factor(leaf.type):factor(geno) 7     116.79   16.684  0.7505 0.07282 0.644
## Residuals             56    1244.97   22.232         0.77626
## Total                 71    1603.81                1.00000
##
## factor(leaf.type)      ***
## factor(geno)           **
## factor(leaf.type):factor(geno)
## Residuals
```

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

if (all(ls() != 'ord.tree')){ord.tree <- nmds.min(nmds(dn.tree,2,2),dims=2)}
spp.vectors <- envfit(ord.tree,spp.tot)
spp.vectors <- envfit(ord.tree,spp.tot[,spp.vectors$vectors$pvals <= 0.05])

mu <- ch.plot(ord.tree,factor(tree.info$geno))
points(mu,col=as.numeric(factor(unique(tree.info$geno))),pch=19,cex=1.5)
plot(spp.vectors,col='darkgrey')
legend('topright',legend=unique(tree.info$geno),
      col=as.numeric(factor(unique(tree.info$geno))),
      pch=19,bty='d',bg='white',box.col='lightgrey')
```



“{r }

```
adonis(distNet(liv.nets)~factor(geno),data=tree.info[tree.info$leaf.type ==
'live',])
```

```
adonis(distNet(sen.nets)~factor(geno),data=tree.info[tree.info$leaf.type ==
'sen',])
```

““

Leaf-type has a marginal affect on the centrality of the network

```
### Following the stats shown here: http://conjugateprior.org/2013/01/formulae-in-r-anova/

library(bipartite)
```



```

library(lme4)
### centrality
tree.cen <- unlist(lapply(tree.nets,function(x) centralization(x,FUN='degree'))))
tree.mod <- dget(file='../data/tree.mod') # see src/treeMods.R

tree.mod[tree.mod == 0] <- 0.5

### incorrect handling of error from pairing with trees
## summary(aov(tree.cen~tree+factor(leaf.type)*factor(geno),data=tree.info))
## summary(aov(tree.mod~tree+factor(leaf.type)*factor(geno),data=tree.info))

summary(aov(tree.mod~(factor(geno)*factor(leaf.type)) + Error(tree / (factor(geno) * factor(leaf.type))))

##
## Error: tree
##               Df Sum Sq Mean Sq F value Pr(>F)
## factor(geno)   7  0.1821  0.02601    2.052  0.0833 .
## Residuals     28  0.3550  0.01268
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Error: tree:factor(leaf.type)
##               Df Sum Sq Mean Sq F value Pr(>F)
## factor(leaf.type)      1  0.0988  0.09884    8.325  0.00745 **
## factor(geno):factor(leaf.type)  7  0.1269  0.01812    1.526  0.19914
## Residuals             28  0.3325  0.01187
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

summary(aov(tree.cen~(factor(geno)*factor(leaf.type)) + Error(tree / (factor(geno) * factor(leaf.type))))

##
## Error: tree
##               Df Sum Sq Mean Sq F value Pr(>F)
## factor(geno)   7  0.5161  0.07373    0.859   0.55
## Residuals     28  2.4047  0.08588
##
## Error: tree:factor(leaf.type)
##               Df Sum Sq Mean Sq F value Pr(>F)
## factor(leaf.type)      1  0.1380  0.13802    2.168   0.152
## factor(geno):factor(leaf.type)  7  0.6164  0.08805    1.383   0.251
## Residuals             28  1.7824  0.06366

```

Genotype does not directly influence senescence, but may indirectly influence senescence through pb.

```

summary(aov(I(leaves^0.5)~factor(geno)*pb,
            data=data.frame(tree.info,spp.tot)[tree.info$leaf.type == 'sen',]))

```

```

##               Df Sum Sq Mean Sq F value Pr(>F)
## factor(geno)   7  171.2   24.46    1.178  0.3564
## pb             1   98.8   98.82    4.760  0.0406 *

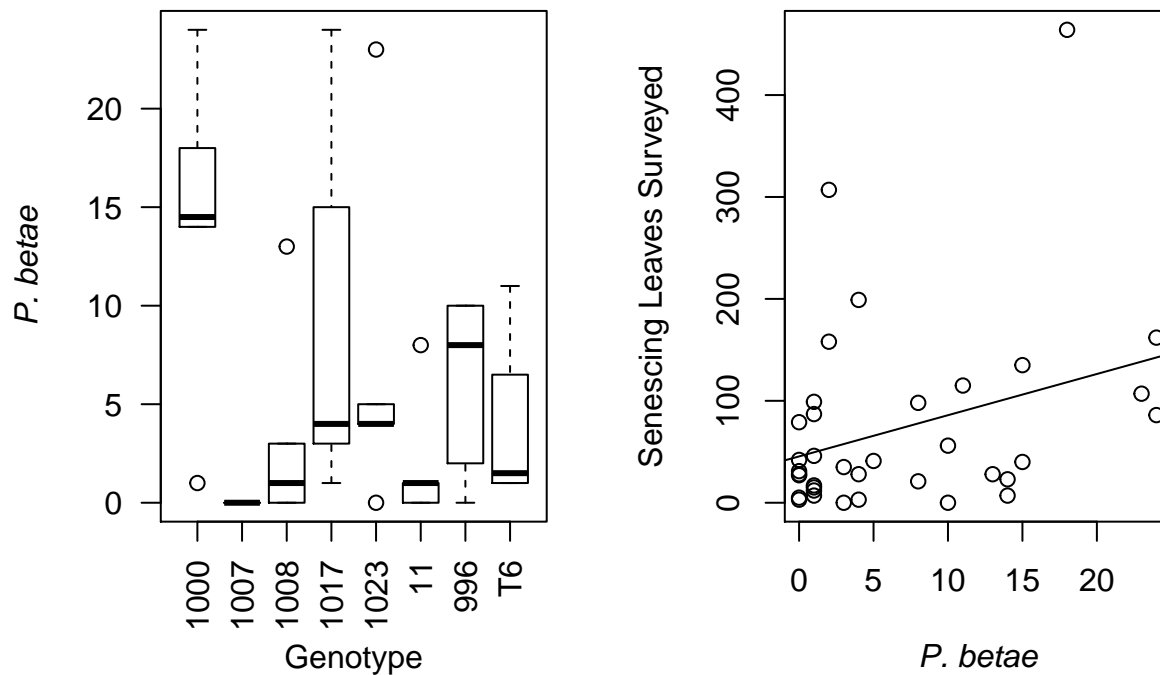
```

```
## factor(geno):pb 6 79.5 13.25 0.638 0.6985
## Residuals 21 436.0 20.76
## ---
## Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
summary(aov(I(pb^0.5) ~ factor(geno),
            data=data.frame(tree.info,spp.tot)[tree.info$leaf.type == 'sen',]))
```

```
##           Df Sum Sq Mean Sq F value Pr(>F)
## factor(geno) 7 30.03 4.290 2.114 0.0751 .
## Residuals 28 56.81 2.029
## ---
## Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
par(mfrow=c(1,2))
plot(pb~geno,
     data=data.frame(tree.info,spp.tot)[tree.info$leaf.type == 'sen',],
     xlab='Genotype',ylab=expression(italic('P. betae')),las=2)
plot(leaves~pb,
     data=data.frame(tree.info,spp.tot)[tree.info$leaf.type == 'sen',],
     xlab=expression(italic('P. betae')),ylab='Senescing Leaves Surveyed')
abline(lm(leaves~pb,data=data.frame(tree.info,spp.tot)[
  tree.info$leaf.type == 'sen',]))
```



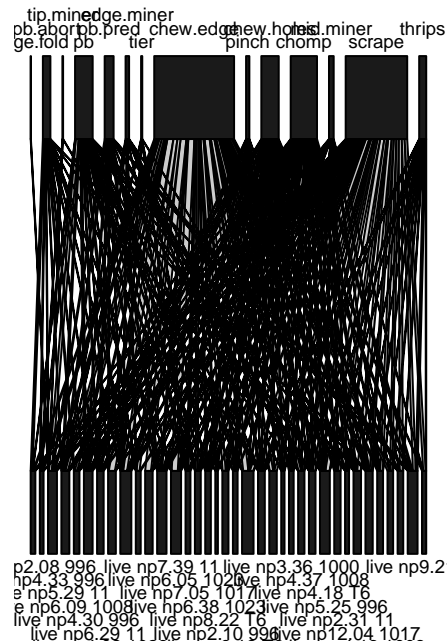
Stand level network modularity

```
liv.bpn <- spp.tot[tree.info$leaf.type == 'live',]
sen.bpn <- spp.tot[tree.info$leaf.type == 'sen',]

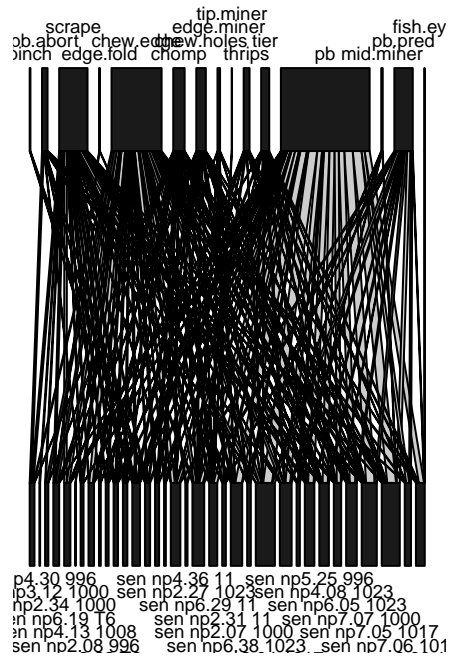
liv.modules <- dget('../data/liv.modules')
sen.modules <- dget('../data/sen.modules')
```

```
par(mfrow=c(1,2))
plotweb(liv.bpn);title(main='Live')
plotweb(sen.bpn);title(main='Senescent')
```

## Live



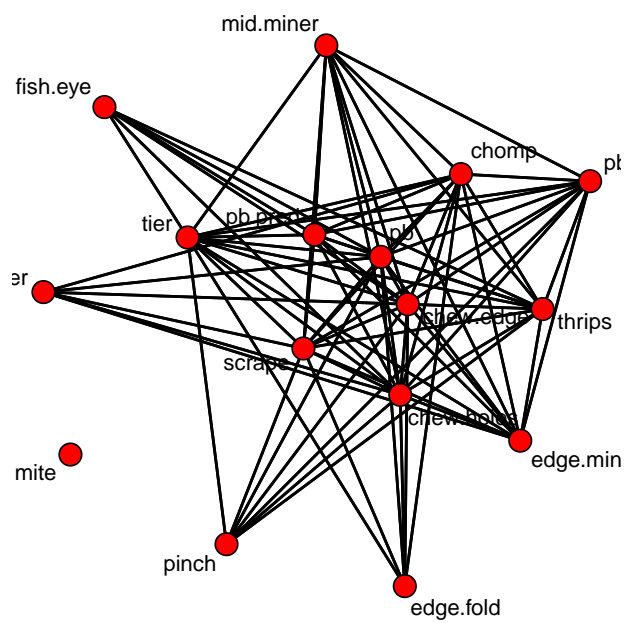
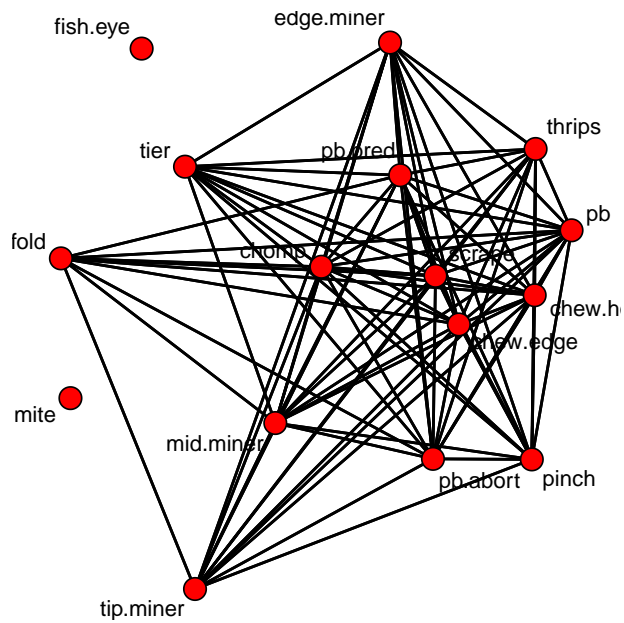
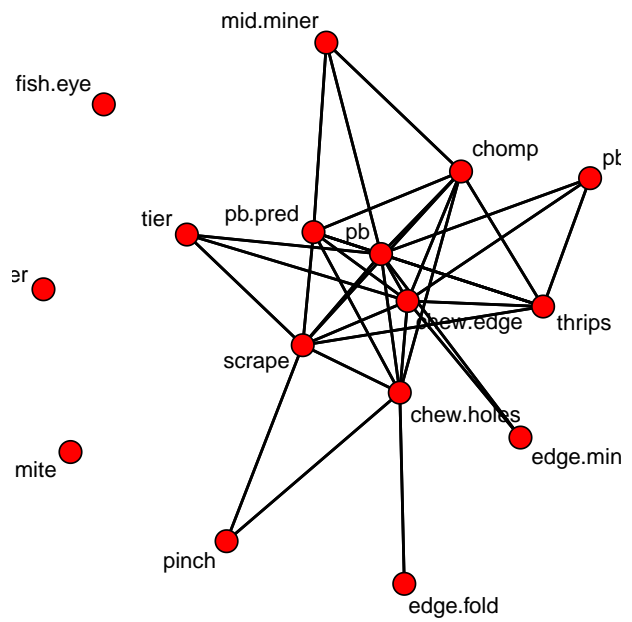
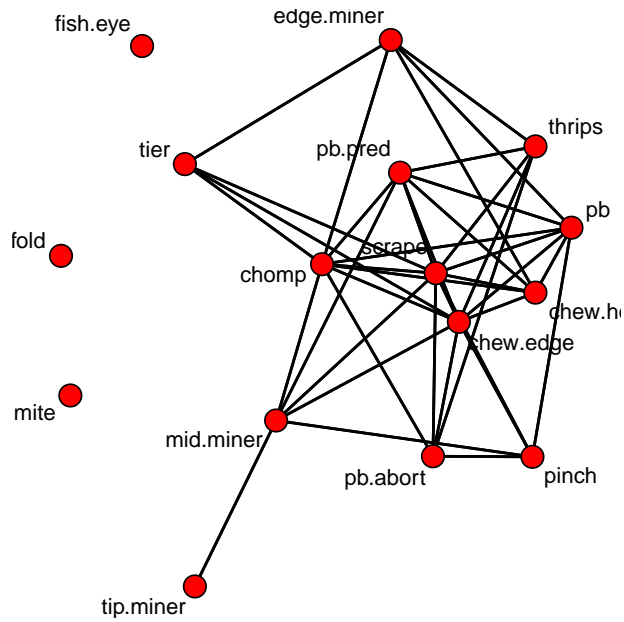
## Senescent



How does the mean interaction network compare to the bipartite to unipartite projection?

```
liv.b2u <- t(liv.bpn) %*% liv.bpn
sen.b2u <- t(sen.bpn) %*% sen.bpn

par(mfrow=c(2,2),mai=rep(0.1,4))
liv.coo <- gplot(liv.mu,gmode='graph',displaylabels=TRUE)
sen.coo <- gplot(sen.mu,gmode='graph',displaylabels=TRUE)
gplot(liv.b2u,coord=liv.coo,gmode='graph',displaylabels=TRUE)
gplot(sen.b2u,coord=sen.coo,gmode='graph',displaylabels=TRUE)
```



```
spp.cen <- rbind(liv.spc,sen.spc)

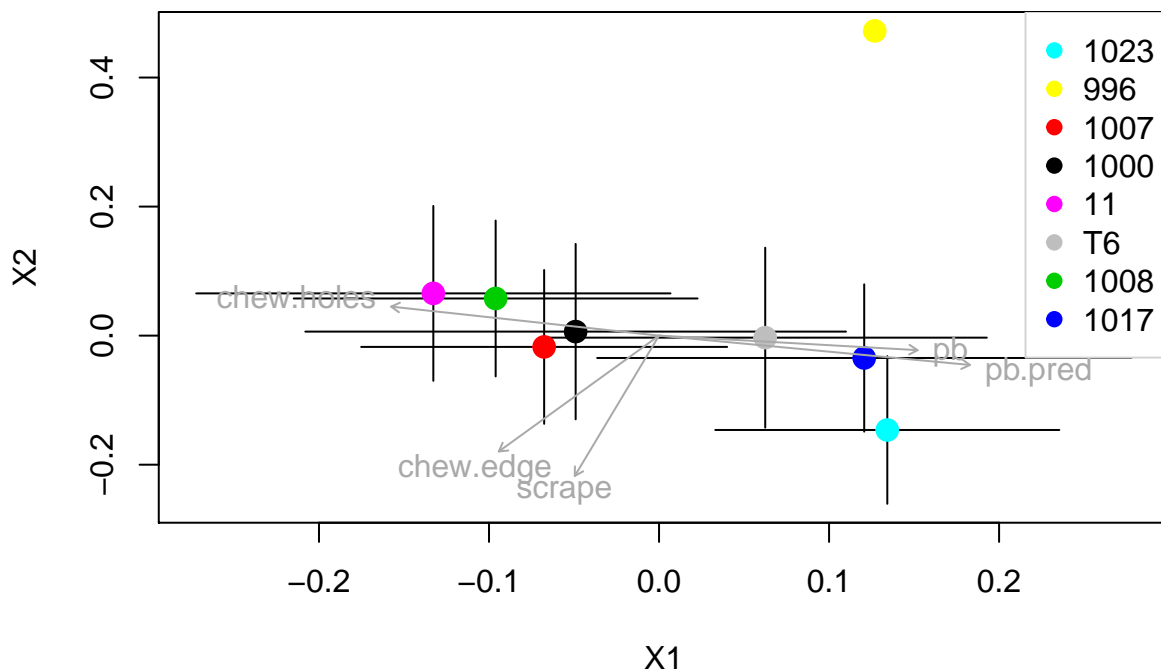
adonis(spp.cen~factor(leaf.type)*factor(geno),data=tree.info, strata=tree.info$tree,method='euc')

##
## Call:
## adonis(formula = spp.cen ~ factor(leaf.type) * factor(geno),      data = tree.info, method = "euc",
##
## Blocks: strata
## Permutation: free
## Number of permutations: 999
##
## Terms added sequentially (first to last)
```

```
##
##
##      Df SumsOfSqs MeanSqs F.Model    R2 Pr(>F)
## factor(leaf.type)      1    2.532 2.53199  5.6131 0.07561 0.001
## factor(geno)           7    2.491 0.35587  0.7889 0.07438 0.002
## factor(leaf.type):factor(geno) 7    3.206 0.45799  1.0153 0.09573 0.195
## Residuals            56   25.261 0.45108      0.75428
## Total                71   33.490      1.00000
##
## factor(leaf.type)      ***
## factor(geno)           **
## factor(leaf.type):factor(geno)
## Residuals
## Total
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
if (!(any(ls() == 'spc.ord'))){
  spc.ord <- nmds.min(nmds(dist(spp.cen),3,3))
  spc.env <- envfit(spc.ord,spp.cen,strata=tree.info$tree)
  spp.env <- envfit(spc.ord,spp.cen[,spc.env$vectors$pvals <= 0.05])
}

mu <- ch.plot(spc.ord,factor(tree.info$geno))
points(mu,col=as.numeric(factor(unique(tree.info$geno))),pch=19,cex=1.5)
plot(spp.env,col='darkgrey')
legend('topright',legend=unique(tree.info$geno),
      col=as.numeric(factor(unique(tree.info$geno))),
      pch=19,bty='d',bg='white',box.col='lightgrey')
```



What does the unipartite projection look like for the trees and genotypes? This question isn't very interesting since the effect of genotype doesn't differ between live and senescing leaves.