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 inpact 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 genetially based trait, also contributed to interaction network structure, also altering the distribution of interactions in the networks.
3. Genetically based resistance to *Pemphigus betae* (a gall forming aphid), also played a major 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 though 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:

```r
### 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  "
```

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

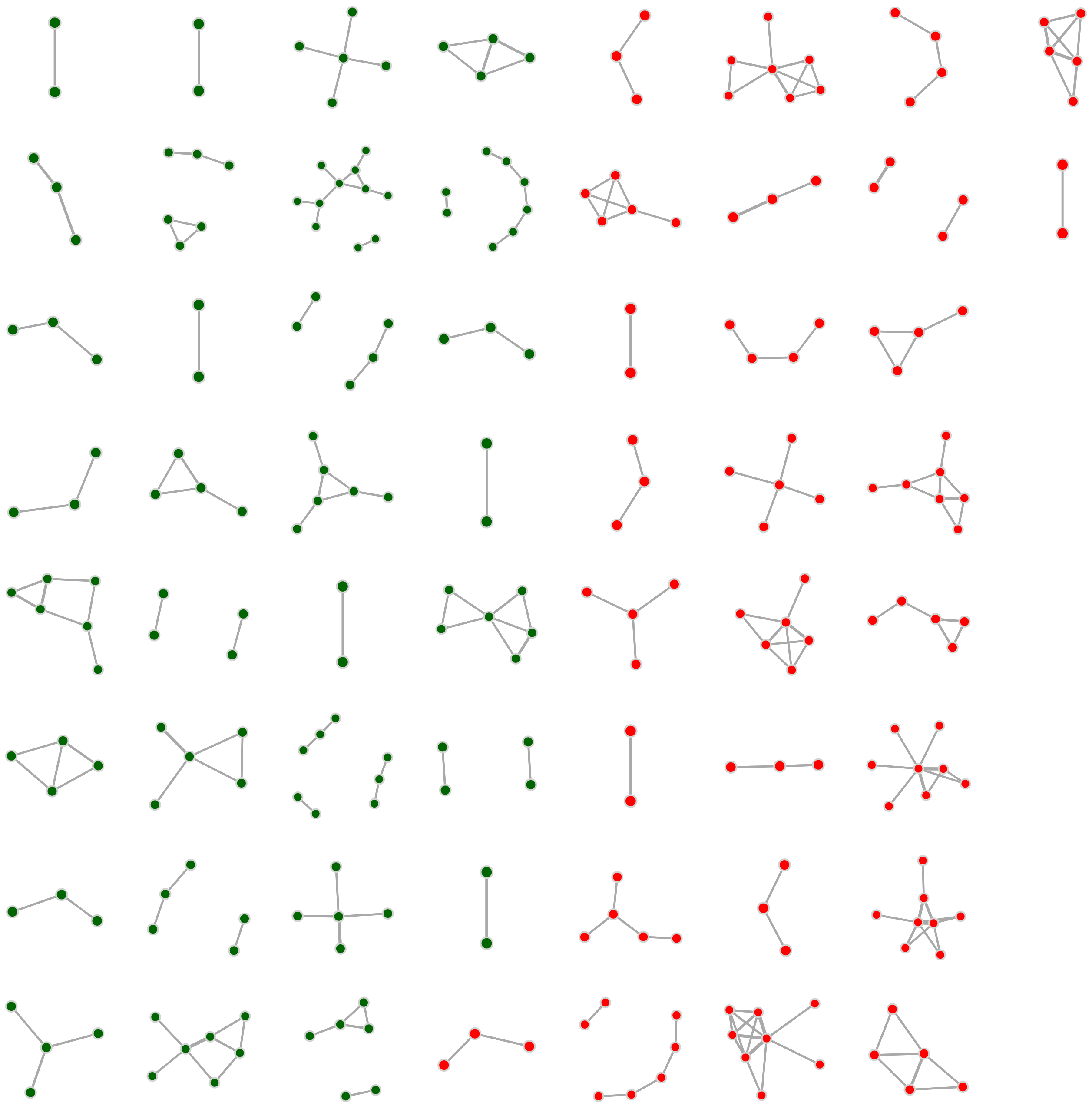
```
##                     Length Class        Mode  
## live np12.04 1017 "16"   "data.frame" "list"
## live np12.07 1017 "16"   "data.frame" "list"
## live np13.10 1017 "16"   "data.frame" "list"
## live np2.07 1000  "16"   "data.frame" "list"
## live np2.08 996   "16"   "data.frame" "list"
## live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

```r
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.

```r
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)
    }
}
```

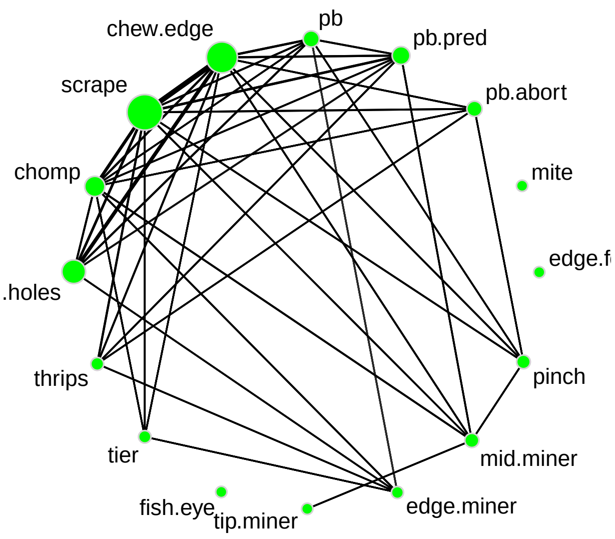


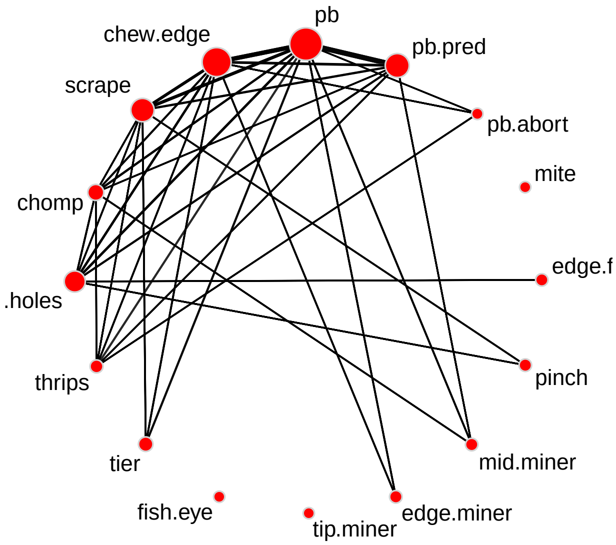
```
t.test(I(liv.cen-sen.cen))
```

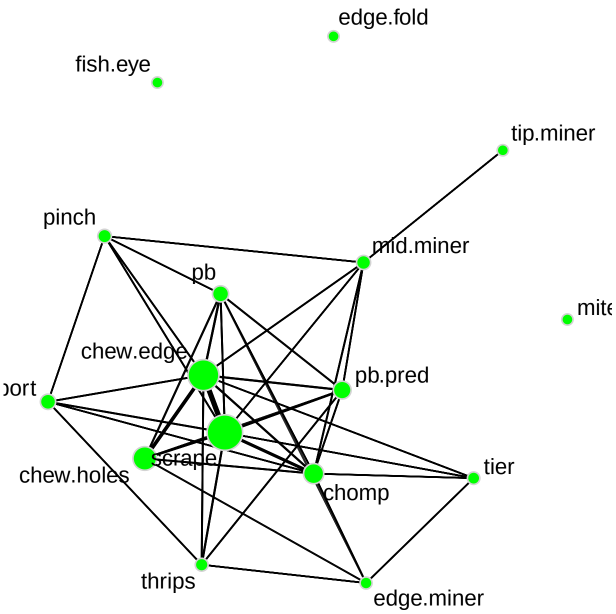
```
##
##  One Sample t-test
##
## data:  I(liv.cen - sen.cen)
## t = -1.3324, df = 35, p-value = 0.1914
## alternative hypothesis: true mean is not equal to 0
## 95 percent confidence interval:
##  -0.22098995  0.04585768
## sample estimates:
##   mean of x
## -0.08756614
```

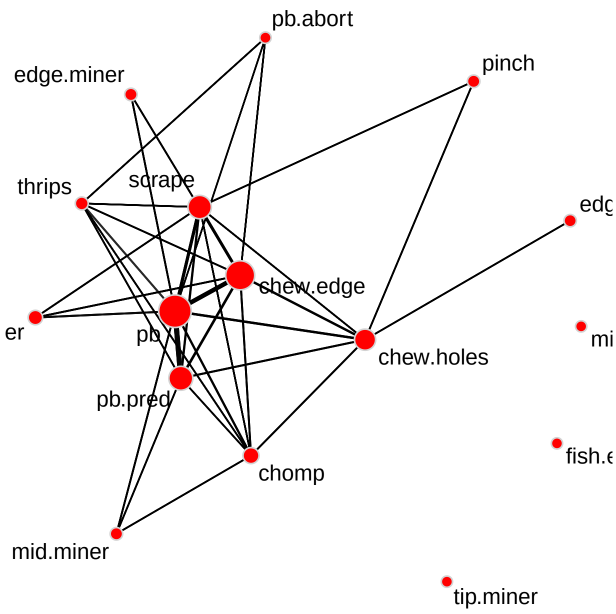
Analyze the mean networks for live and senescent leaves.

```
# 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.cen-sen.cen))
```

```
##
##  Pearson's product-moment correlation
##
## data:  n.lfs and I(liv.cen - sen.cen)
## 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
```

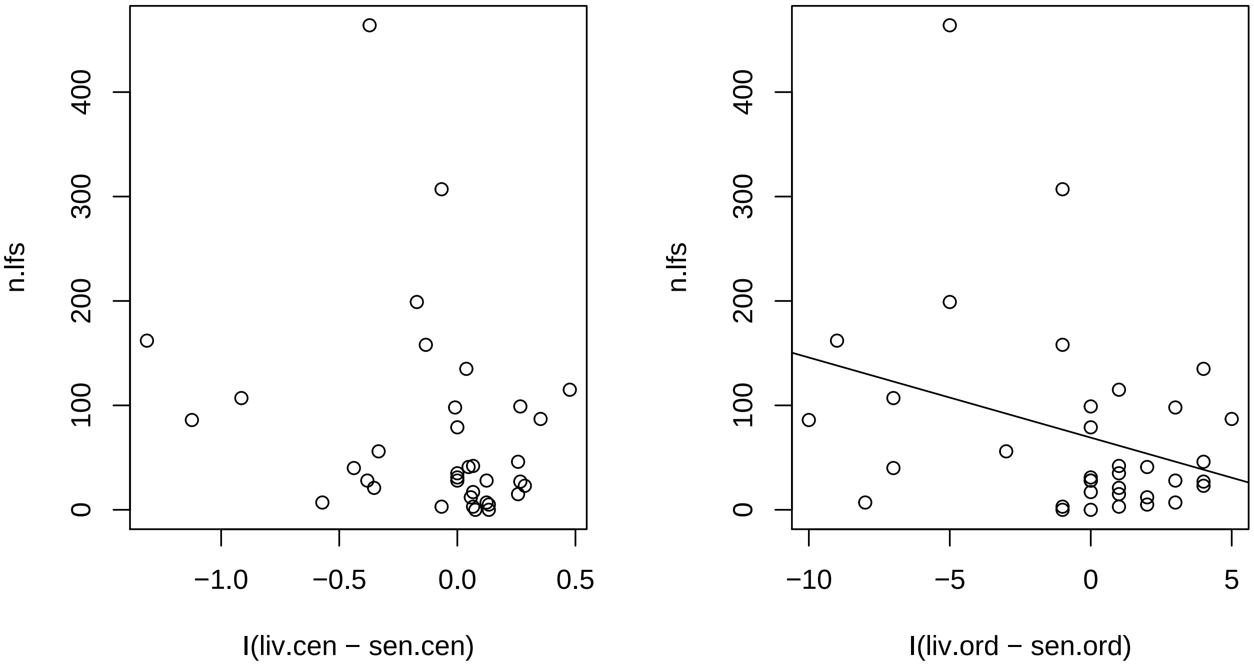
```
cor.test(n.lfs,I(liv.ord-sen.ord))
```

```
##
##  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  0.212
## Residuals 34    946.43  27.836         0.96155
## Total     35    984.28                 1.00000
```

```
par(mfrow=c(1,2))
plot(I(liv.cen-sen.cen),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.

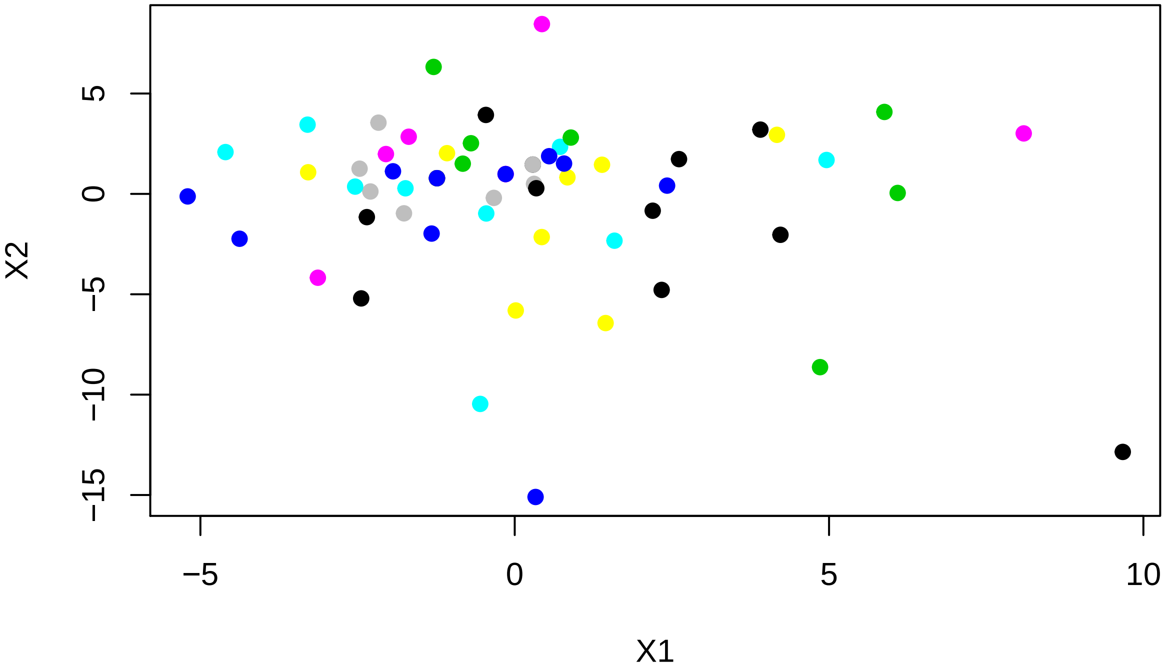
```
library(BiodiversityR)
library(ecodist)
dn.tree <- distNet(tree.nets)
adonis(dn.tree~factor(leaf.type)*factor(geno),data=tree.info, strata=tree.info$tree)
```

```
##
## 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  0.004
## factor(leaf.type):factor(geno)    7    116.79  16.684  0.7505 0.07282  0.658
## 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
```

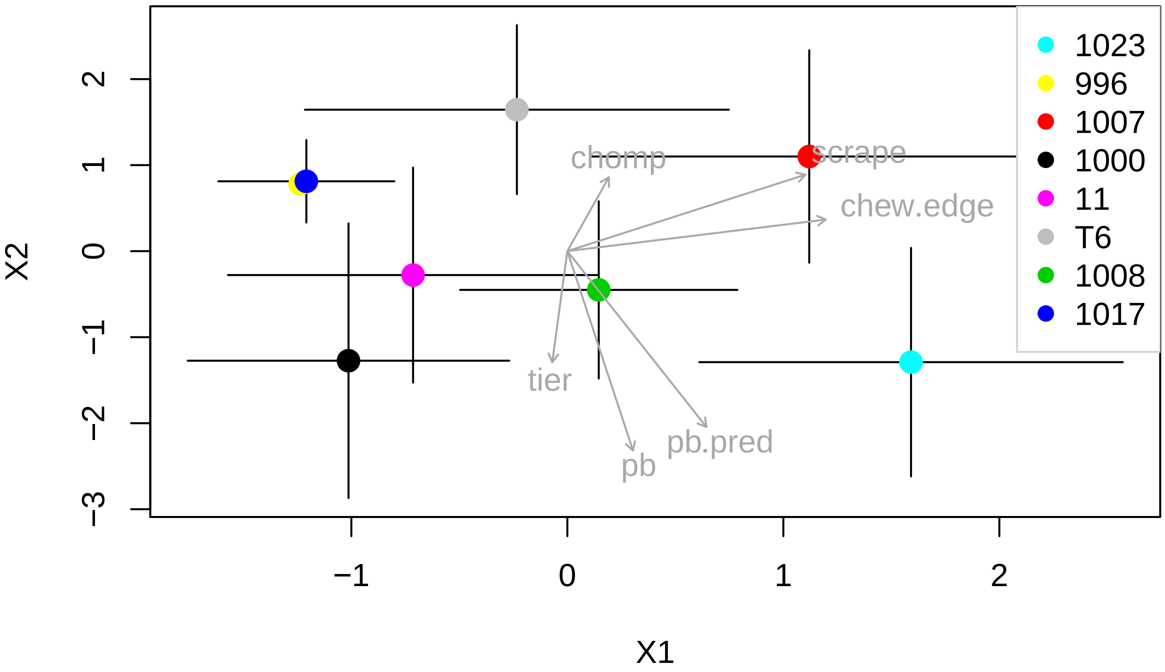
```
ord.tree <- nmds.min(nmds(dn.tree,2,2),dims=2)
```

```
## Using random start configuration
## Using random start configuration
## Using random start configuration
## Using random start configuration
## Using random start configuration
## Using random start configuration
## Using random start configuration
## Using random start configuration
## Using random start configuration
## Using random start configuration
## Minimum stress for given dimensionality:  0.1658217
## r^2 for minimum stress configuration:  0.9397245
```

```
spp.vectors <- envfit(ord.tree,spp.tot)
spp.vectors <- envfit(ord.tree,spp.tot[,spp.vectors$vectors$pvals <= 0.05])

plot(ord.tree,pch=19,
     col=as.numeric(factor(tree.info$geno)))
```



```
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’,])

“‘

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

summary(aov(tree.cen~tree+factor(leaf.type)*factor(geno),data=tree.info))
```

```
##                                 Df Sum Sq Mean Sq F value Pr(>F)
## tree                            35 2.9209 0.08345   1.311  0.232
## factor(leaf.type)                1 0.1380 0.13802   2.168  0.152
## factor(leaf.type):factor(geno)  7 0.6164 0.08805   1.383  0.251
## Residuals                       28 1.7824 0.06366
```

```
summary(aov(tree.mod~tree+factor(leaf.type)*factor(geno),data=tree.info))
```

```
##                                 Df Sum Sq Mean Sq F value   Pr(>F)
## tree                            35 1.0698  0.0306   0.903 0.616910
## factor(leaf.type)                1 0.5749  0.5749  16.976 0.000304 ***
## factor(leaf.type):factor(geno)  7 0.2974  0.0425   1.255 0.307767
## Residuals                       28 0.9482  0.0339
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

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

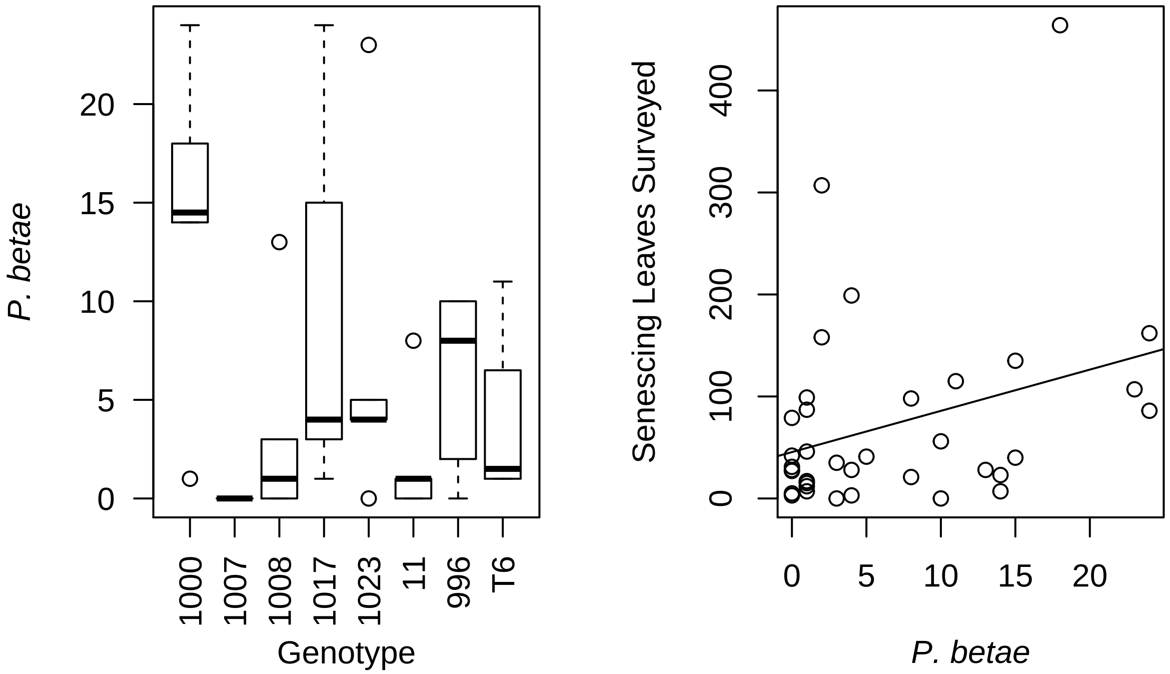
```
summary(aov(I(leaves^0.5)~factor(geno)*pb,
            data=data.frame(tree.info,spp.tot)[tree.info$leaf.type == 'sen',]))
```

```
##                 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',]))
```

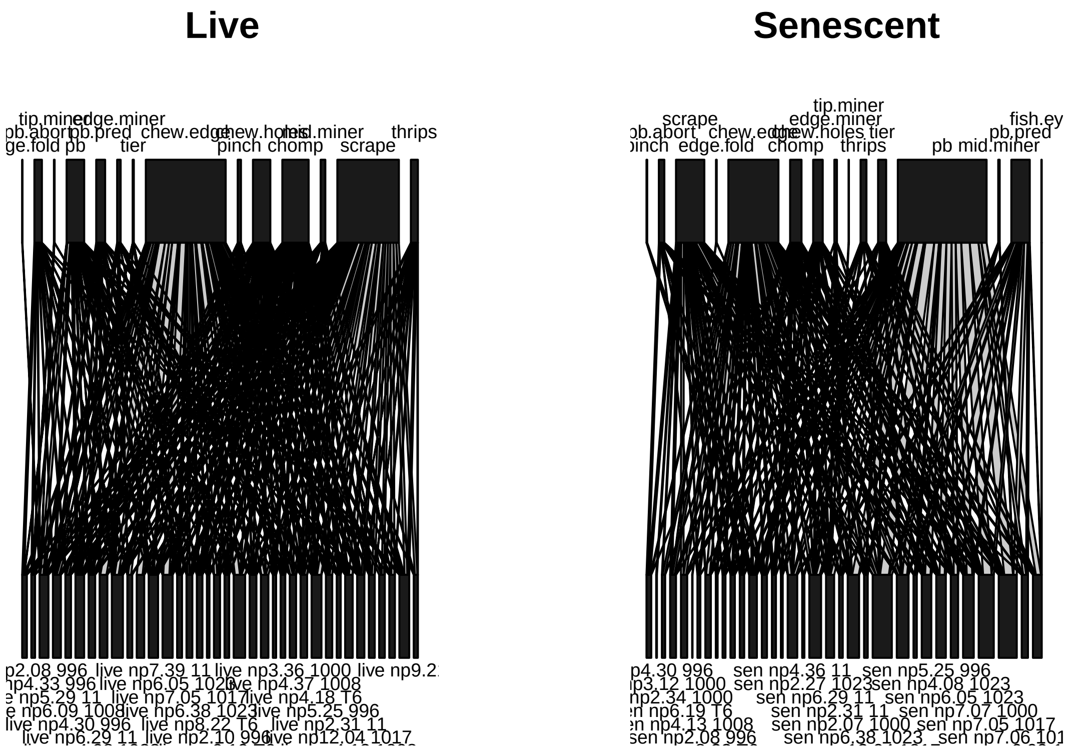
```
##              Df Sum Sq Mean Sq F value Pr(>F)
## factor(geno)  7  30.03   4.290   2.114 0.0751 .
## Residuals    28  56.81   2.029
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
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',]))
```



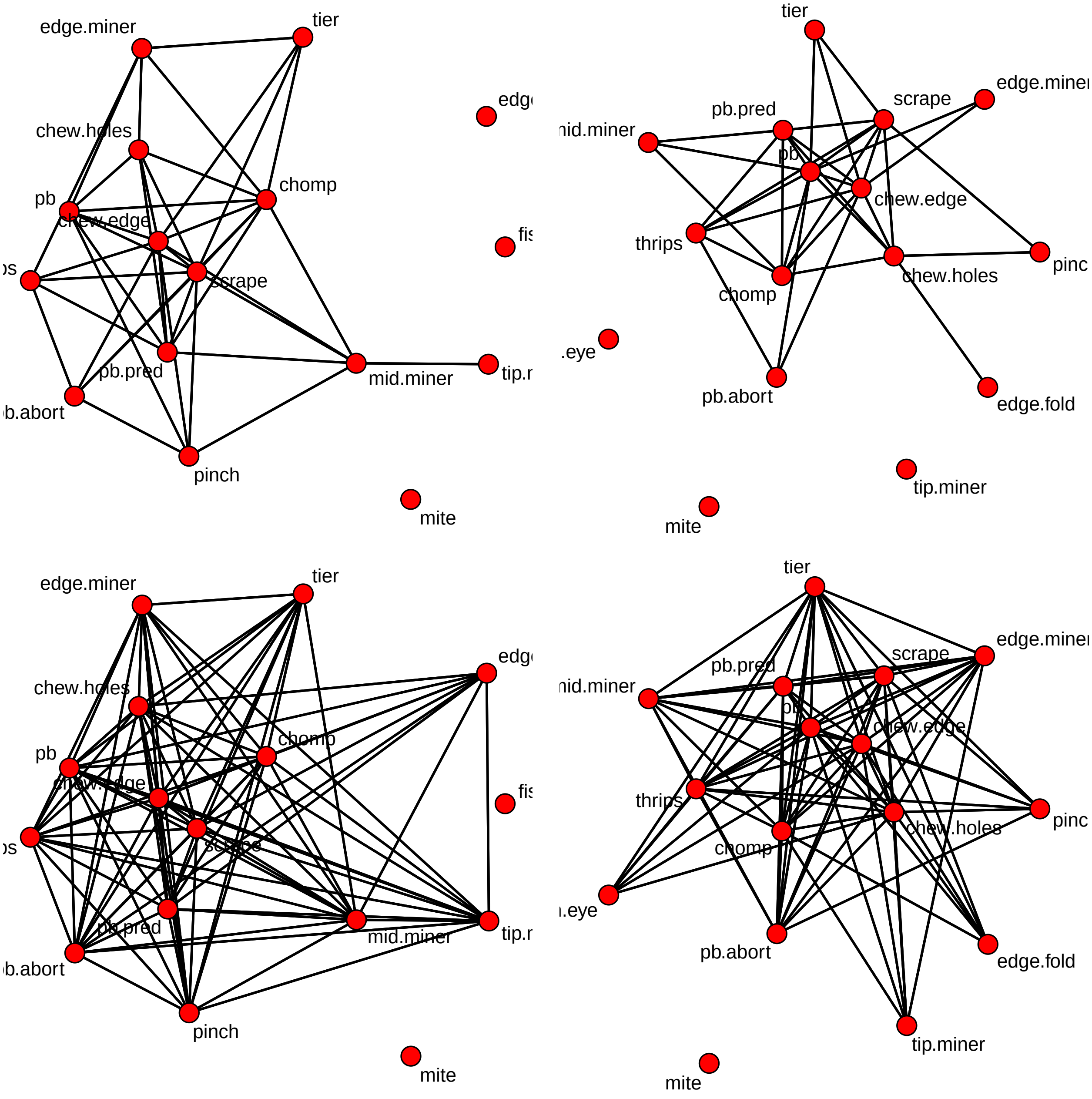
Stand level network modularity

```
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')
```



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

```r
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)
```



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