BIO 682
Quantitative Biology
Spring 2009

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http://www4.nau.edu/shustercourses/BIO682/index.htm

Lecture 13

Diversity Measures

Whittaker (1972) described three terms for measuring biodiversity over spatial scales: alpha, beta, and gamma diversity.

Alpha diversity refers to the diversity within a particular area or ecosystem, and is usually expressed by the number of species (i.e., species richness) in that ecosystem.

For example, we might want to compare species diversity within different ecosystems, such as an undisturbed deciduous wood, a well-established hedgerow bordering a small pasture, and a large arable field.

Diversity Measures

Beta diversity compares the total number of species that are unique to each of the ecosystems being compared.

For example, the beta diversity between the woodland and the hedgerow habitats is 7 (representing the 5 species found in the woodland but not the hedgerow, plus the 2 species found in the hedgerow but not the woodland).

Thus, beta diversity allows us to compare diversity between ecosystems.

Diversity Measures

Gamma diversity is a measure of the overall diversity for the different ecosystems within a region.

For example, the total number of species for the three ecosystems represents the gamma diversity.

Euclidean Distance

The Euclidean distance between points;
in Euclidean n-space, distance is defined as:

$$\sqrt{(p_1 - q_1)^2 + (p_2 - q_2)^2 + \cdots + (p_n - q_n)^2}$$

$$= \sqrt{\sum_{i=1}^{n} (p_i - q_i)^2}.$$

In 2D n = 2 (x,y); In 3D, n = 3 (x,y,z)

The Bray-Curtis Dissimilarity Coefficient

$$BC_{ij} = \sum \frac{|n_{ik} - n_{jk}|}{(n_{ik} + n_{jk})}$$

Where i and j refer to the cell values in each k-th dissimilarity matrix and BCij is the dissimilarity score for that matrix.

The Bray-Curtis Dissimilarity Coefficient

	Value1	Value2	Value3	Value4
Object A	0	3	4	5
Object B	7	6	3	-1

$$d_{BA} = \frac{|0-7|+|3-6|+|4-3|+|5+1|}{(0+7)+(3+6)+(4+3)+(5-1)}$$

$$= \frac{7+3+1+6}{7+9+7+4} = \frac{17}{27} = 0.630$$

Stress

$$S = \left\{ \left[\sum_{i<j} [d_{ij} - \hat{d}_{ij}]^2 \right] \Big/ \left[\sum_{i<j} d_{ij}{}^2 \right] \right\}^{1/2}.$$

Where d_{ij} is the distance in ordination space between samples i and j, and

for each sample pair, i and j; the regression between the distance measure and distance produces a value, d^ij

Questions:

Is it possible to detect differences in in the communities of arthropods that assemble on different genotypes of the same host tree?

Questions:

Is it possible to detect the community level consequences of selection on foundation tree species?

When community level selection occurs, how can the significance of its effects be measured?

The Central Prediction of Community Genetics

(Whitham et al. 2003, 2006)

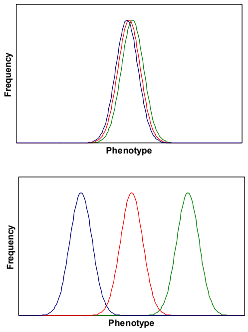
Genetically based interactions between foundation species and their associated organisms generate particular community phenotypes.

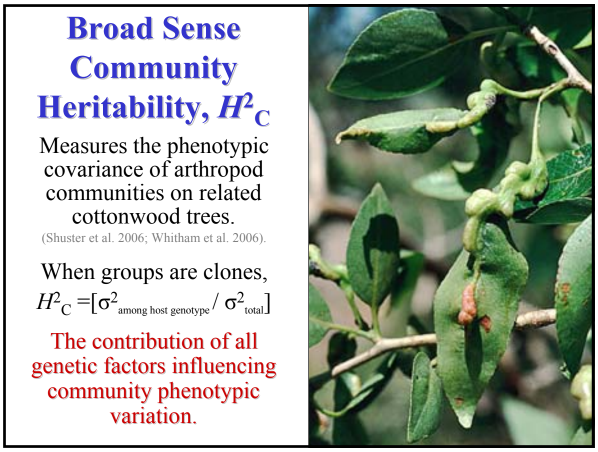
Partitioning Variance Components

ANOVA Asks:

Does the variance exist mainly ***within groups*** (are group means similar?)

Does it exist mainly ***among groups*** (are group means different?)





Broad Sense Community Heritability, H^2_C

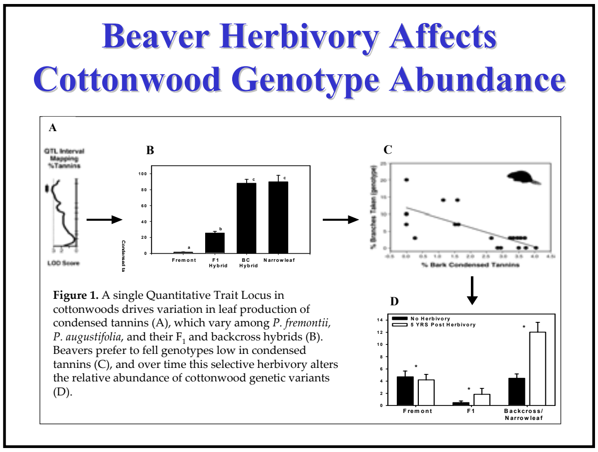
Measures the phenotypic covariance of arthropod communities on related cottonwood trees.

(Shuster et al. 2006; Whitham et al. 2006).

When groups are clones,

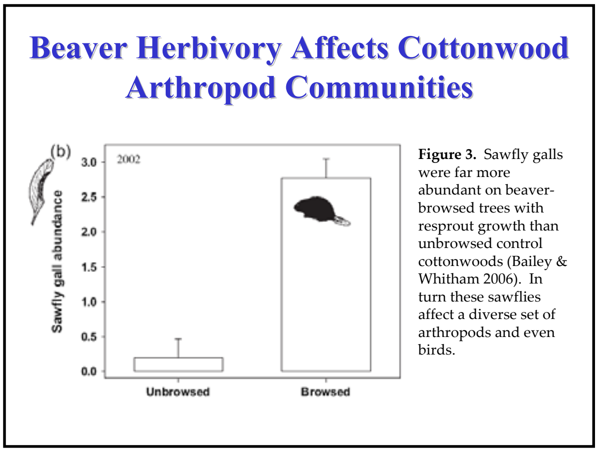
$H^2_C = [\sigma^2_{\text{among host genotype}} / \sigma^2_{\text{total}}]$

The contribution of all genetic factors influencing community phenotypic variation.



Beaver Herbivory Affects Cottonwood Genotype Abundance

Figure 1. A single Quantitative Trait Locus in cottonwoods drives variation in leaf production of condensed tannins (A), which vary among *P. fremontii*, *P. augustifolia*, and their F_1 and backcross hybrids (B). Beavers prefer to fell genotypes low in condensed tannins (C), and over time this selective herbivory alters the relative abundance of cottonwood genetic variants (D).



Beaver Herbivory Affects Cottonwood Arthropod Communities

Figure 3. Sawfly galls were far more abundant on beaver-browsed trees with resprout growth than unbrowsed control cottonwoods (Bailey & Whitham 2006). In turn these sawflies affect a diverse set of arthropods and even birds.

Beaver Effects Extend to Other Foundation Species

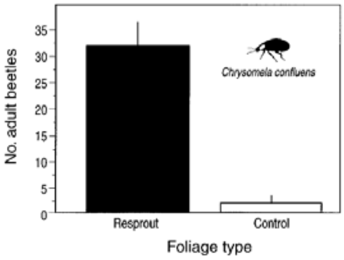
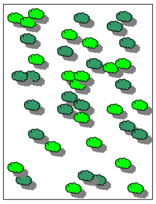


Figure 4. Beetles *Chrysomela confluens* were 15 times more abundant on cottonwood resprouts than on adjacent nonresprouts because they sequester the induced defenses of the tree for their own defense (Martinsen et al. 1998).

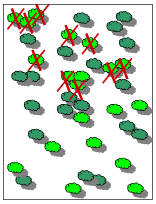
Questions:

Is it possible to detect the community level consequences of selection on foundation species?

When community level selection occurs, how can the significance of its effects be measured?

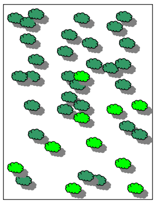


Selective herbivory removes non-resistant tree genotypes



● = resistant
○ = non-resistant

These are replaced by resistant tree genotypes (vegetatively or not)



Which Phenotypes?

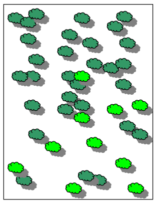
Trees (genotypic and phenotypic variation)

Arthropods (Genotypic and phenotypic variation)

Communities

(phenotypic variation)

What to Measure?



$X_{1j.} = \Sigma\, p_{1jk} x_{1jk}$

$V_{x1j.} = \Sigma\, p_{1jk}(X_{1j} - x_{1jk})^2$

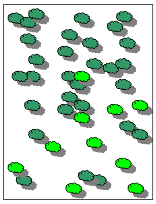
x_{ijk} = the NMDS score of the k-th community in the j-th stand of trees in the i-th treatment.

p_{ijk} = the frequency of the k-th community in the j-th stand of trees in the i-th treatment.

$X_{ij.}$ = the average community phenotype in the j-th stand of trees in the i-th treatment.

$V_{Xij.}$ = the variance in community phenotype in the j-th stand of trees in the i-th treatment.

Two Treatments, n Replicates

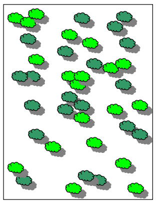


With beavers

$X_{1j.} = \Sigma\, p_{1jk} x_{1jk}$

$V_{x1j.} = \Sigma\, p_{1jk}(X_{1j} - x_{1jk})^2$

X_{11} V_{x11}	X_{21} V_{x21}
X_{12} V_{x12}	X_{22} V_{x22}
X_{13} V_{x13}	X_{23} V_{x23}
⋮	⋮
X_{1n} V_{x1n}	X_{2n} V_{x2n}



Without beavers

$X_{2j.} = \Sigma\, p_{2jk} x_{2jk}$

$V_{x2j.} = \Sigma\, p_{2jk}(X_{2j} - x_{2jk})^2$

The Total Variance

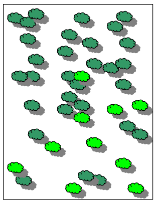
$$V_{total} = V_{within} + V_{among}$$

= The *average of the variances* within the classes (groups)

\+

The *variance of the averages* among the classes (groups)

With beavers



x_{11} V_{x11}

x_{12} V_{x12}

x_{13} V_{x13}

⋮

x_{1n} V_{x1n}

The Variance Within Stands

$$V_{1within} = \Sigma V_{1j.}/n_{stand} = \Sigma p_{1j.}V_{1j.}$$

The Variance Among Stands

$$V_{1among} = \Sigma(X_{1..} - X_{1j.})^2/n_{stand} = \Sigma\, p_{1j}(X_{1..} - X_{1j.})^2$$

The Total Variance

$$V_{1total} = V_{1within} + V_{1among}$$

The Treatment Average

$$\mathbf{X}_{1..} = \Sigma\, p_{1jk}\, x_{1jk}$$

The Variance Within Stands

$$V_{2within} = \Sigma V_{2j.}/n_{stand} = \Sigma p_{2j.}V_{2j.}$$

The Variance Among Stands

$$V_{1among} = \Sigma(X_{2..} - X_{2j.})^2/n_{stand} = \Sigma\, p_{2j}(X_{2..} - X_{2j.})^2$$

The Total Variance

$$V_{2total} = V_{2within} + V_{2among}$$

The Treatment Average

$$\mathbf{X}_{2..} = \Sigma\, p_{2jk}\, x_{2jk}$$

x_{21} V_{x21}

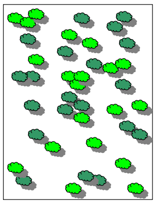
x_{22} V_{x22}

x_{23} V_{x23}

⋮

x_{2n} V_{x2n}

Without beavers



The Grand Average

$$\mathbf{X}_{...} = \Sigma\, p_{ijk}\, x_{ijk}$$

The Total Variance

$$V_{total} = V_{within} + V_{among}$$

= The *average of the variances*
within the classes (groups)
+
The *variance of the averages*
among the classes (groups)

The Total Variance

$$V_{total} = V_{within} + V_{among}$$

$$= \{[V_{1total}+V_{2total}]/2\} + \{\Sigma\ (X_{...}-X_{i..})^2]/2\}$$

Wade 1976

"Just as individual selection requires that there be differences between individuals, group selection requires that there be differences between populations.

…this between-populations variance is the *sine qua non* of group selection."

Has Community-Level Selection Occurred?

$$V_{1among} / V_{total}$$

= The fraction of the total variance in community phenotype that arises due to beaver herbivory

Questions:

Is it possible to detect the community level consequences of selection on foundation species?

When community level selection occurs, how can the significance of its effects be measured?

F-tests

Snedecor and Cochran, 1983

The formula for *F* (for R.A. Fisher) is

$$F = \frac{s_1^2}{s_2^2}$$

The variance are usually arranged so that F>1.
i.e., $s_1^2 > s_2^2$.

$F = \frac{s_1^2}{s_2^2}$

Degrees of Freedom

Sokal and Rohlf 1981

The upper variance (among groups) is based on the variance of some number of averages.

Usually, $v_1 = a(k - 1)$,

Where k = the number of individuals per group

Or, v_1 may = $(n - 1)$.

The lower variance (within groups) is based on the mean of some number of variances.

Usually, $v_2 = a - 1$

Where a = the number of variances.

In Most Cases

You test for significant differences in the variances (4 steps).

1) Invoke a null hypothesis that the two variances are from the same population. (i.e., they are not statistically different)
2) Calculate the F value (the ratio of the two variances)
3) Look up the table value of F for the degrees of freedom used to calculate both variances and for a given confidence level.
4) If the calculated F is greater than the table value, then the null hypothesis is not correct.

Conclusions:

It IS possible to detect the community level consequences of selection on foundation species.

When community level selection occurs, the significance of its effects can be measured using variance ratio tests.

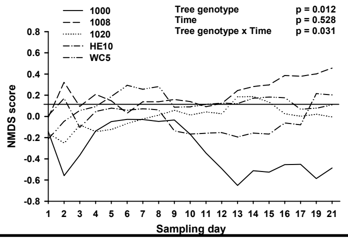
Chaitophorus on Narrowleaf

(Wooley et al. almost in review)

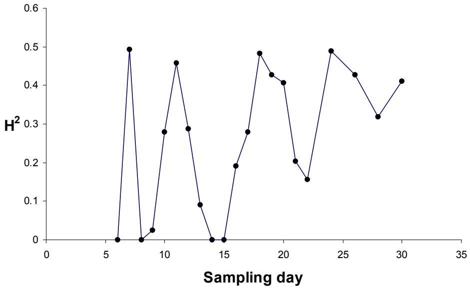
Four aphid clones on 5 *P. angustifolia* genotypes

Clone abundances monitored over 32 days

Figure 2



Heritability of aphid genotypic community structure over time



The Opportunity for Selection

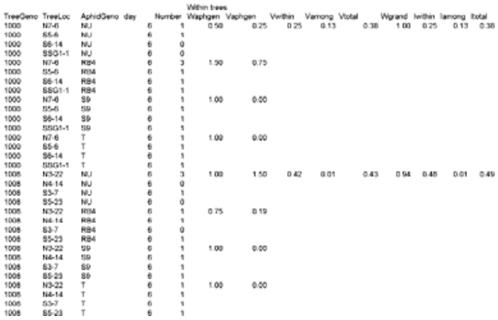
(Crow 1958, 1962; Wade 1979)

$$I = V_W/W^2 = V_w$$

Compares the fitness of favored individuals *relative* to the population before selection.

The **variance in relative fitness**, V_w, provides an empirical estimate for selection's strength.

The Opportunity for Selection on Community Phenotype



					Within trees								
TreeGeno	TreeLoc	AphidGeno	day	Number	Waphgen	Vaphgen	Vwithin	Vamong	Vtotal	Wgrand	Iwithin	Iamong	Itotal
1000	N7-6	NU	6	1	0.50	0.25	0.25	0.13	0.38	1.00	0.25	0.13	0.38
1000	S5-6	NU	6	1									
1000	S6-14	NU	6	0									
1000	SSG1-1	NU	6	0									
1000	N7-6	RB4	6	3	1.50	0.75							
1000	S5-6	RB4	6	1									
1000	S6-14	RB4	6	1									
1000	SSG1-1	RB4	6	1									
1000	N7-6	S9	6	1	1.00	0.00							
1000	S5-6	S9	6	1									
1000	S6-14	S9	6	1									
1000	SSG1-1	S9	6	1									
1000	N7-6	T	6	1	1.00	0.00							
1000	S5-6	T	6	1									
1000	S6-14	T	6	1									
1000	SSG1-1	T	6	1									
1008	N3-22	NU	6	3	1.00	1.50	0.42	0.01	0.43	0.94	0.48	0.01	0.49
1008	N4-14	NU	6	0									
1008	S3-7	NU	6	1									
1008	S5-23	NU	6	0									
1008	N3-22	RB4	6	1	0.75	0.19							
1008	N4-14	RB4	6	1									
1008	S3-7	RB4	6	0									
1008	S5-23	RB4	6	1									
1008	N3-22	S9	6	1	1.00	0.00							
1008	N4-14	S9	6	1									
1008	S3-7	S9	6	1									
1008	S5-23	S9	6	1									
1008	N3-22	T	6	1	1.00	0.00							
1008	N4-14	T	6	1									
1008	S3-7	T	6	1									
1008	S5-23	T	6	1									

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