

Community Heritability

**Measures the Evolutionary Consequences
of Indirect Genetic Effects on Community
and Ecosystem Structure**

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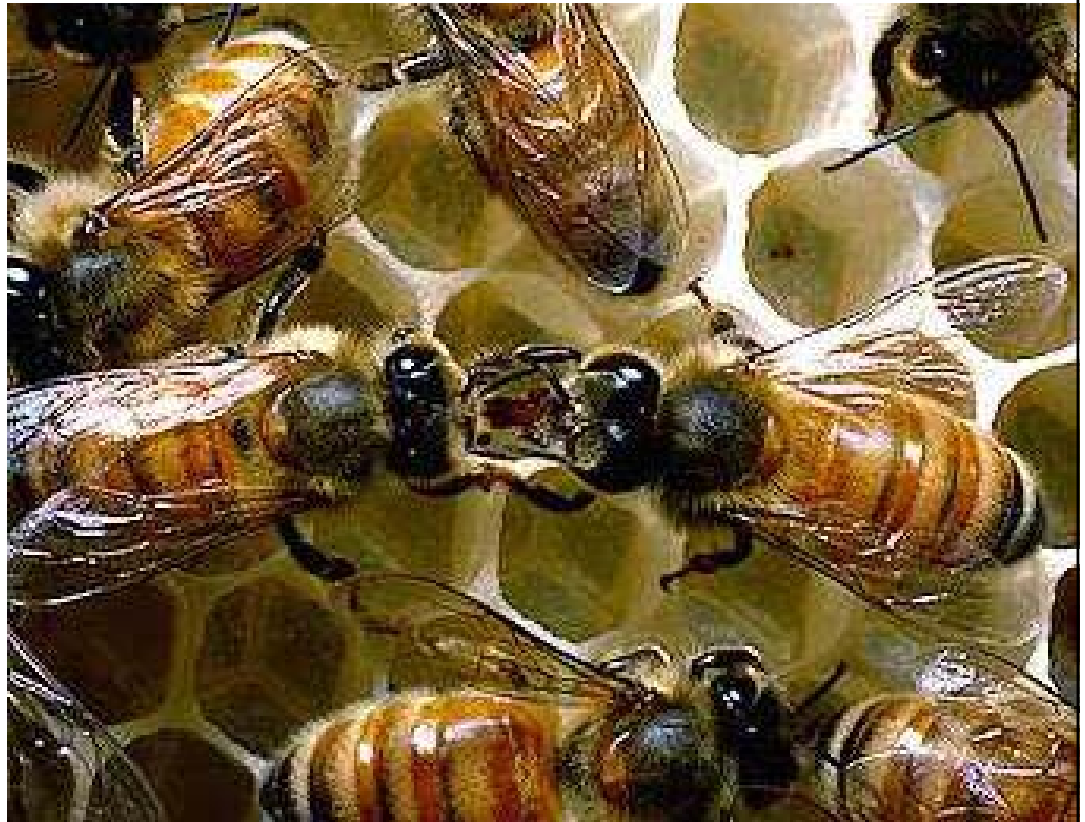
Community Ecology

Considers outcome of interactions among species.

But has yet to incorporate evolutionary insights gained from studies of multi-level selection within species.



**When
individuals
live within
groups,**



conspecific interactions may have significant
indirect genetic effects (IGEs)

(Moore et al. 1997; Goodnight & Stevens 1997; Wolf et al. 1998)



Indirect Genetic Effects (IGEs)

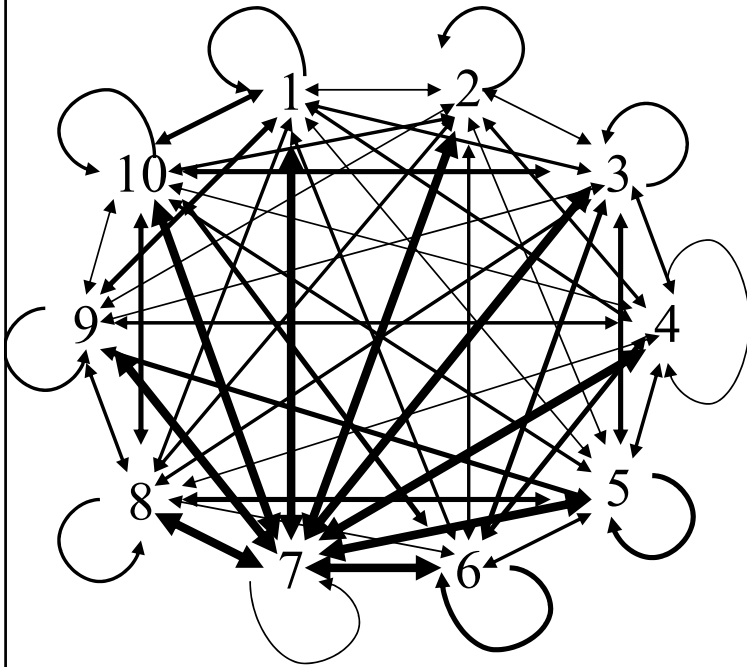
The fitness consequences
of *genetically-based
interactions* among
individuals in the same
species.

IGEs are now considered
important in group and
social evolution

(Wolf et al. 1999; Agrawal et al. 2001; Wade
2003).

An Analogous Mechanism

Involves genetic interactions among individuals in ***different species***.



Genetic differences ***among communities*** are likely to arise.

When the fitness consequences of genetic interactions ***among species*** changes the population frequencies of alleles involved in interactions,

Genetic interactions among species and the fitness effects they impose are likely to undergo ***continuous change***.

Interspecific Indirect Genetic Effects (IIGEs)

The fitness consequences of genetically-based interactions among individuals in *different* species.

IIGEs provide a basis for communities to *evolve* genetically and *differentiate* demographically.

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



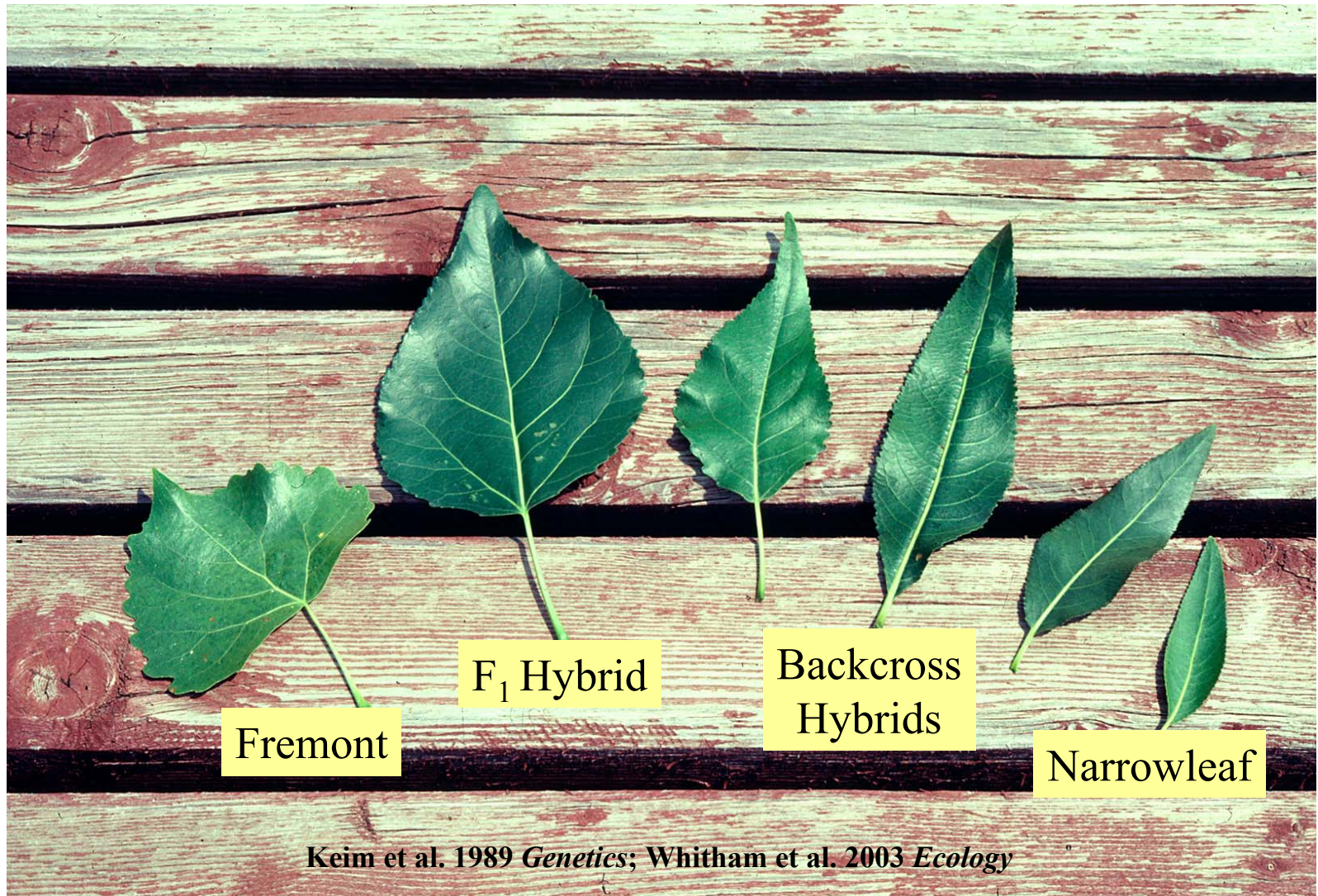
Three Points:

1. Interspecific indirect genetic effects (IIGEs) can occur between plants and arthropods.
2. A genetic basis for arthropod community phenotype on cottonwood is measurable as H^2_C .
3. Significant H^2_C indicates that community-level selection has occurred; community evolution is likely underway.

Cottonwoods (*Populus* spp.) on Weber River, Utah



Unidirectional Introgression in Cottonwoods



Keim et al. 1989 *Genetics*; Whitham et al. 2003 *Ecology*

Genetic Linkage Map of *Populus*

QTL Mapping

Leaf Chlorophyll

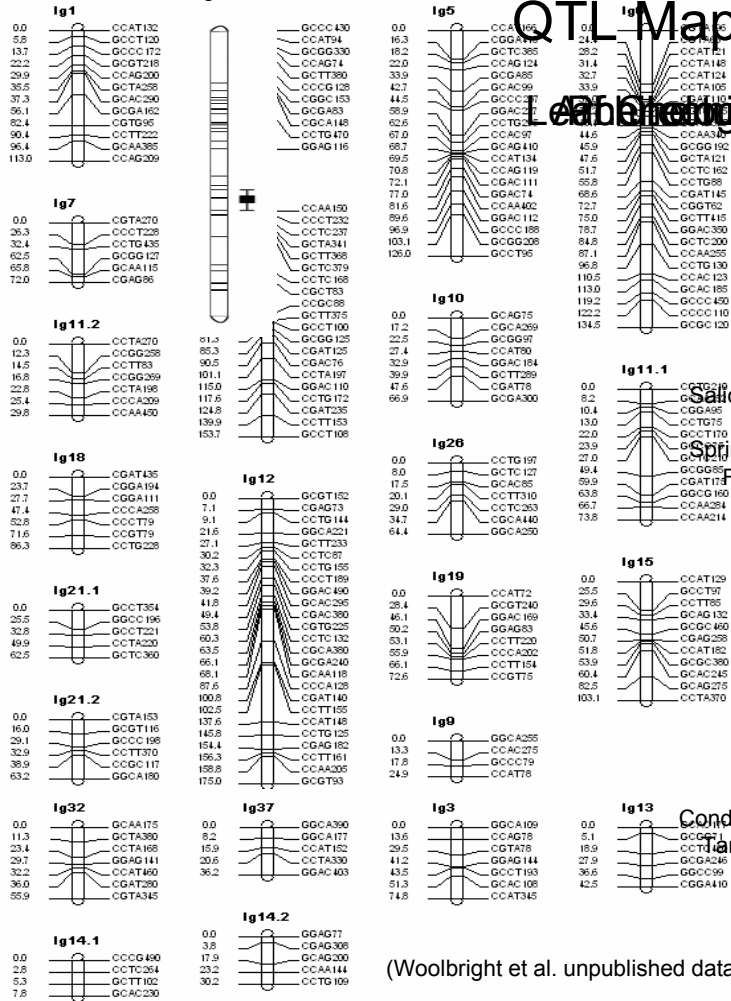
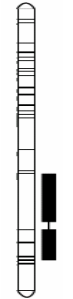
Ig1



Ig8



Ig12



Salicortin

Spring Leaf Flush

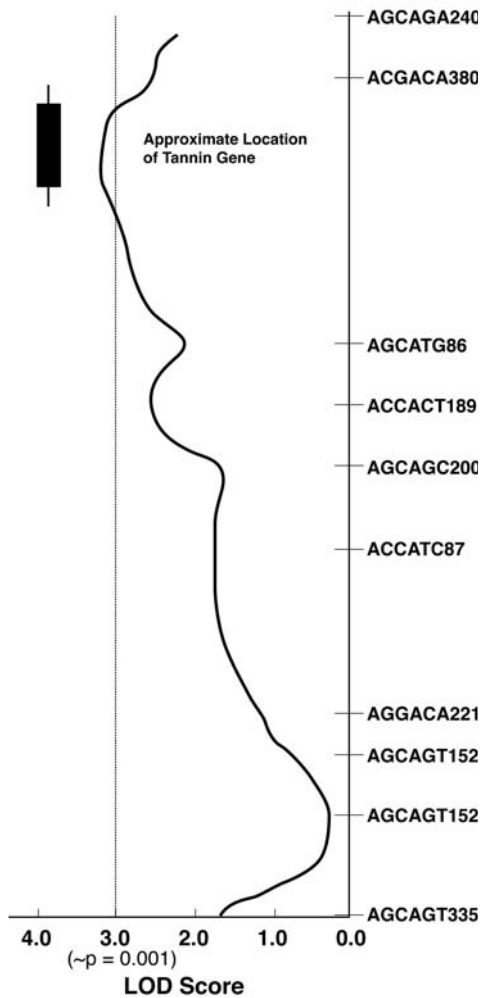
Second Year Branch Number

Condensed Tannin

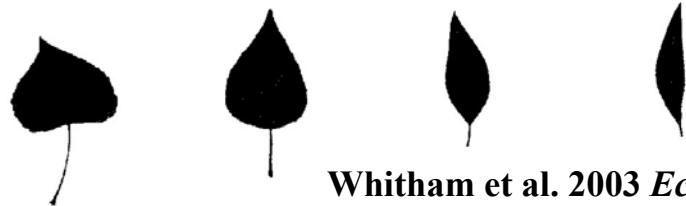
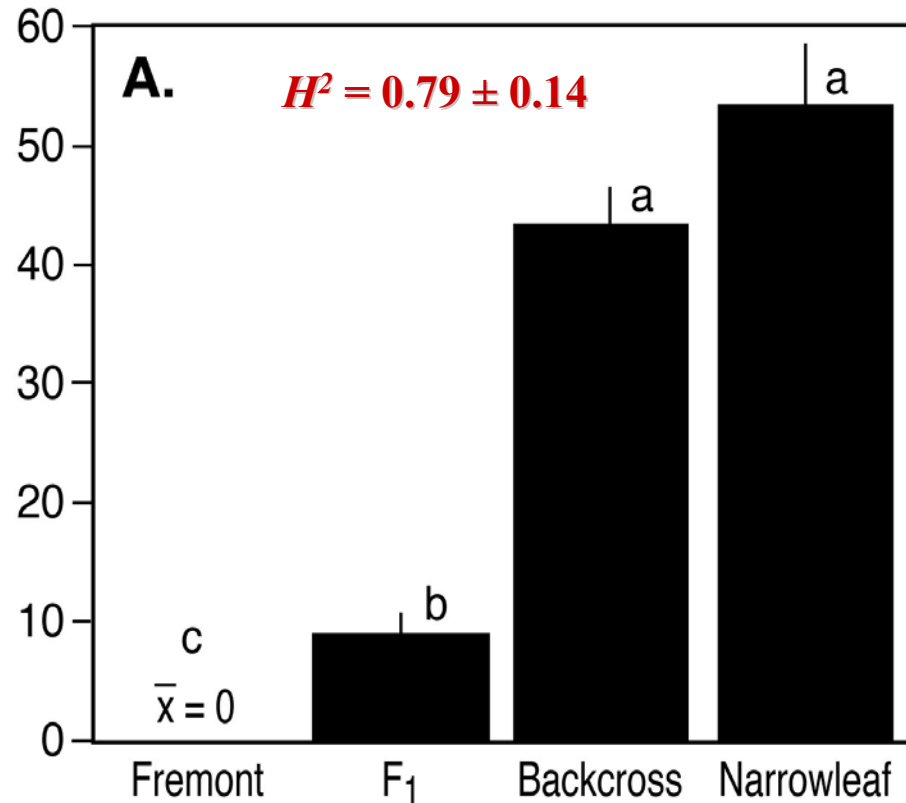
(Woolbright et al. unpublished data)

Cottonwood Phytochemistry Has a Genetic Basis

QTL Interval Mapping



Tannin Concentration (mg/g leaf material)

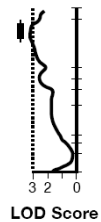


Whitham et al. 2003 *Ecology*

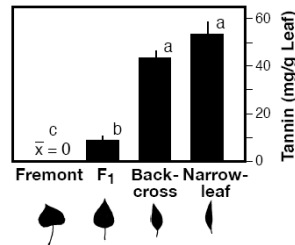
**Tannins
affect
diverse
taxa at all
trophic
levels**

**Create 3
different
phenotypes**

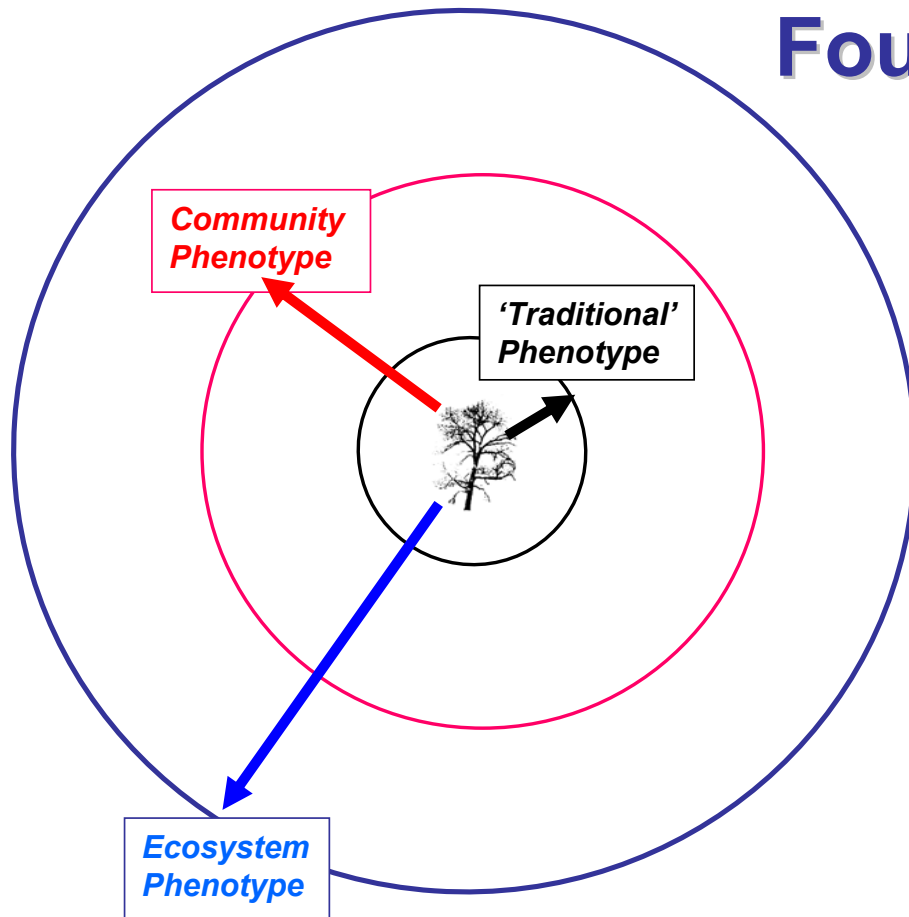
**A. QTL Interval Mapping
of % Tannins**



**B. Traditional Phenotype of
Tannin Production**



Cottonwood Trees as Foundation Species



Species that *structure a community* by creating locally stable conditions for other species

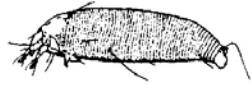
By *modulating and stabilizing* fundamental ecosystem processes.

Shuster et al. 2006 Evolution

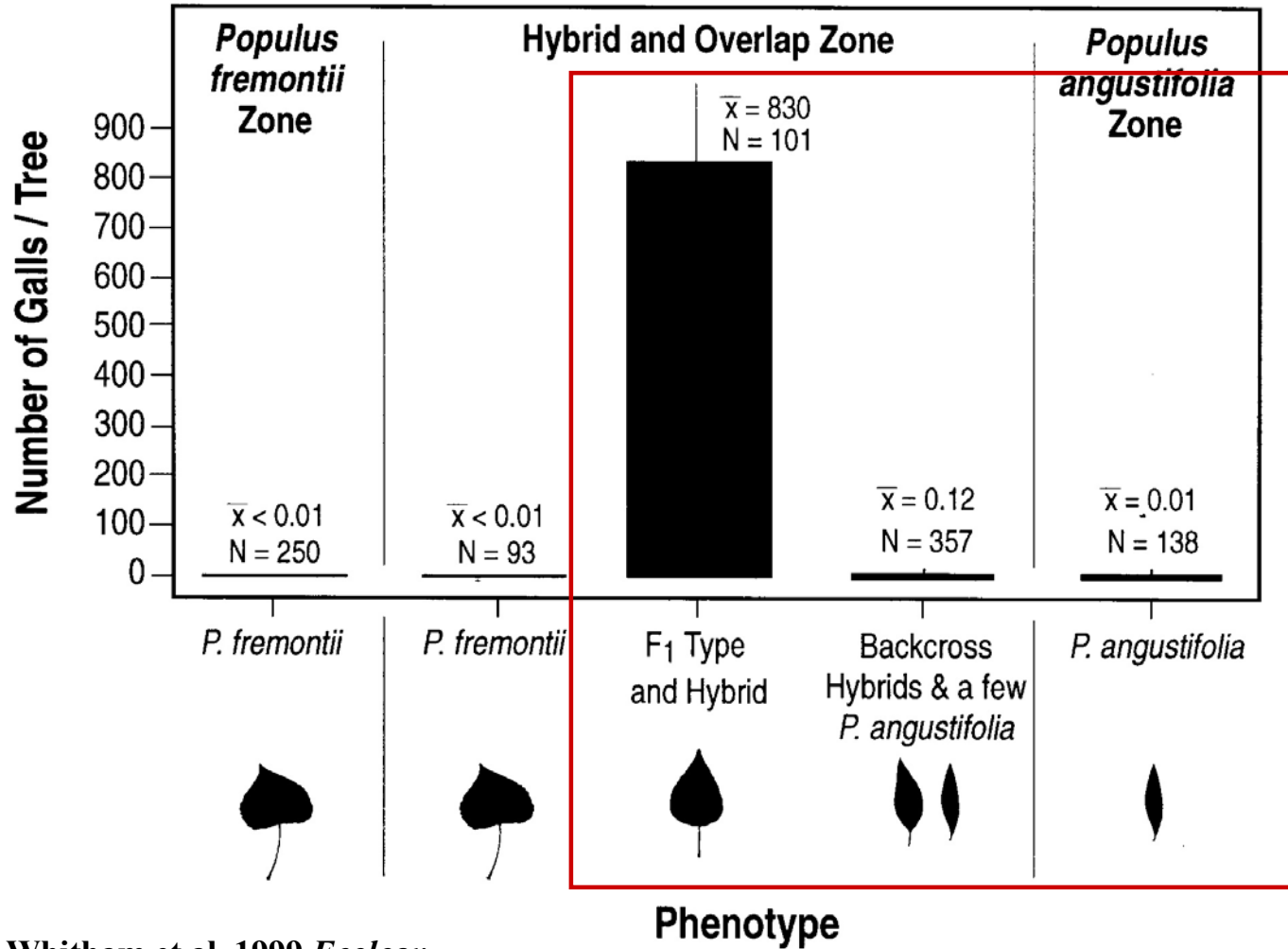
Whitham et al. 2003 Ecology, Whitham et al. 2006 Nature Reviews Genetics

Bud Gall Mite (*Aceria parapopuli*)



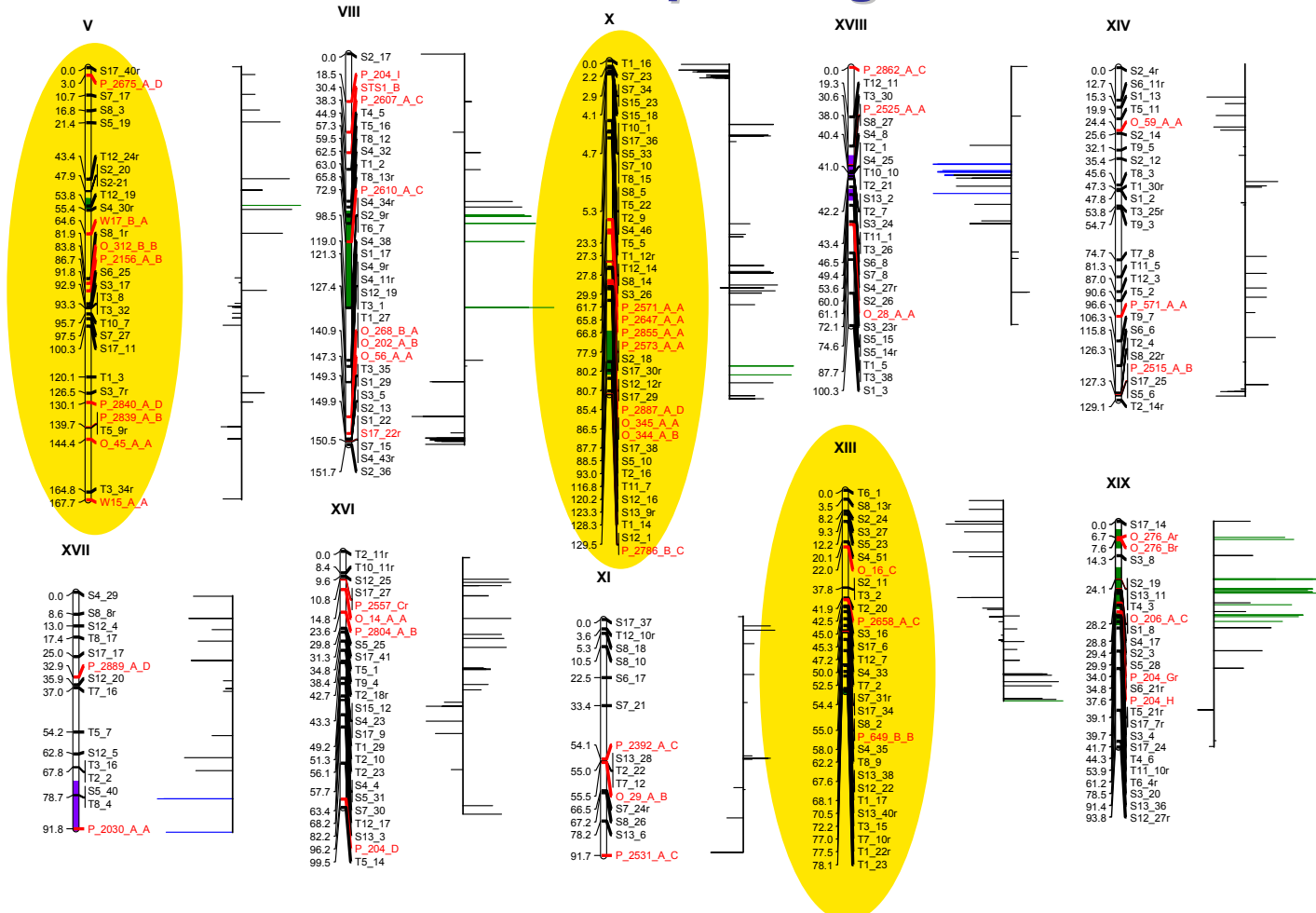


Bud Gall Mite (*Aceria parapopuli*)



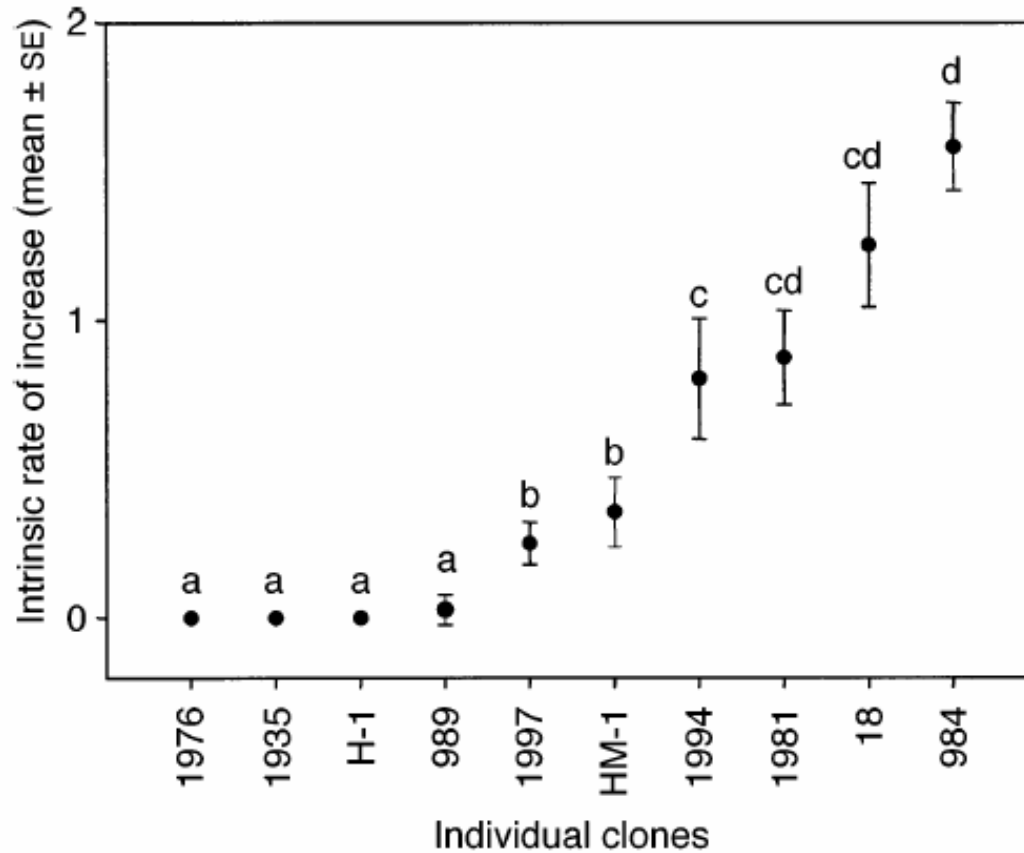
Whitham et al. 1999 *Ecology*

Location of mite susceptibility markers within the *Populus* genome



Scott Woolbright, Gery Allan, Steve DiFazio & the Oak Ridge National Lab Plant Genomics Group

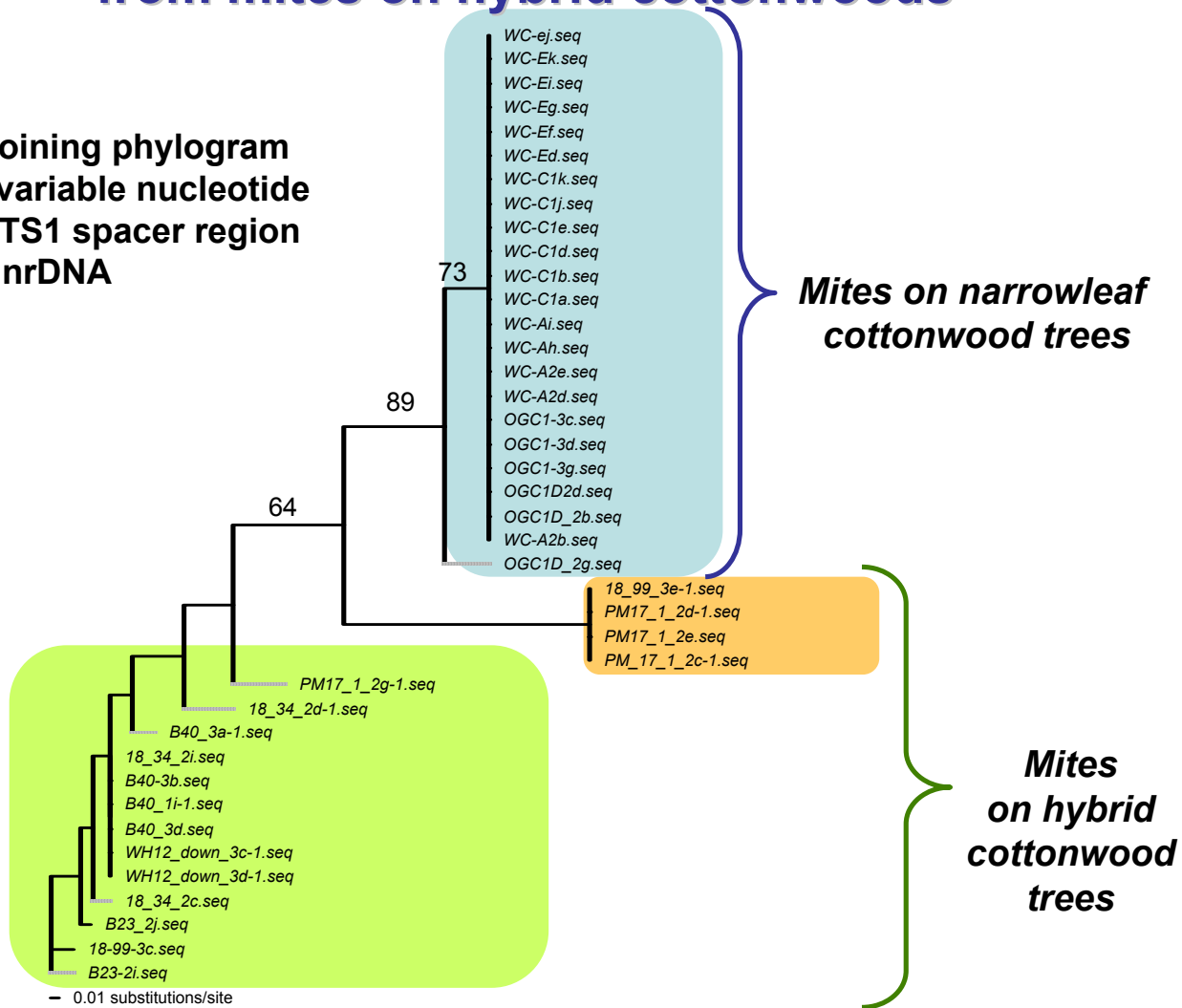
Genetic variation in cottonwoods influences mite fitness



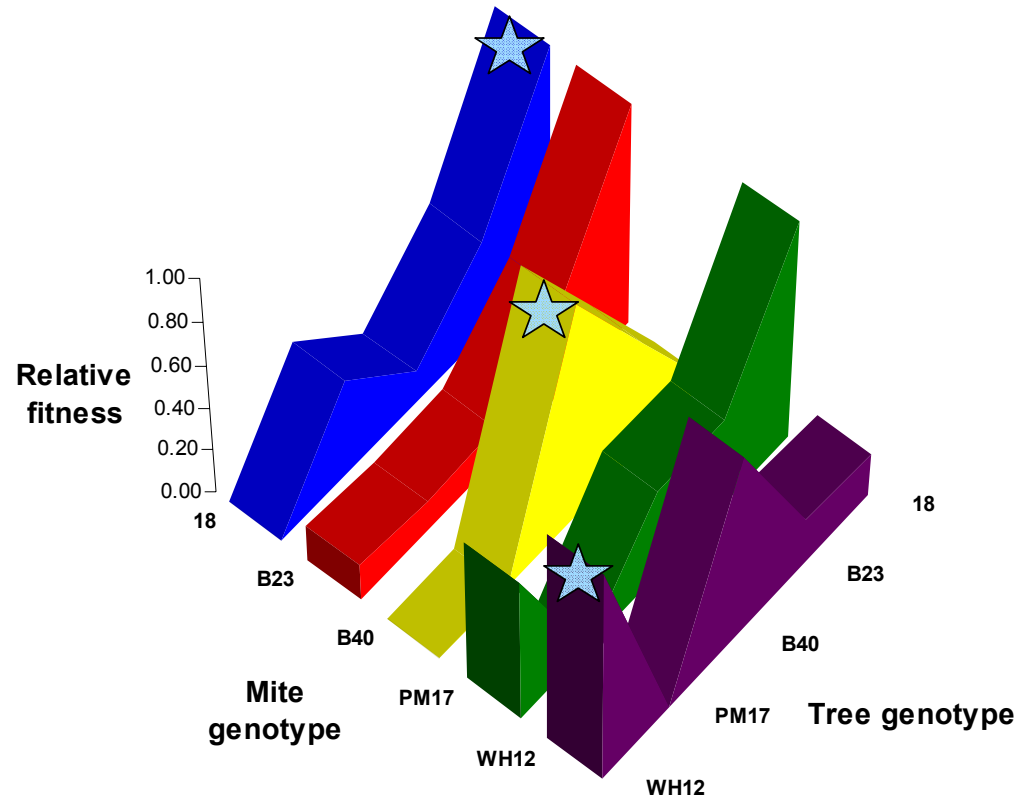
McIntyre & Whitham 2003, *Ecology*

Mites on narrowleaf cottonwood are genetically distinct from mites on hybrid cottonwoods

Neighbor-joining phylogram based on 9 variable nucleotide sites from ITS1 spacer region nrDNA

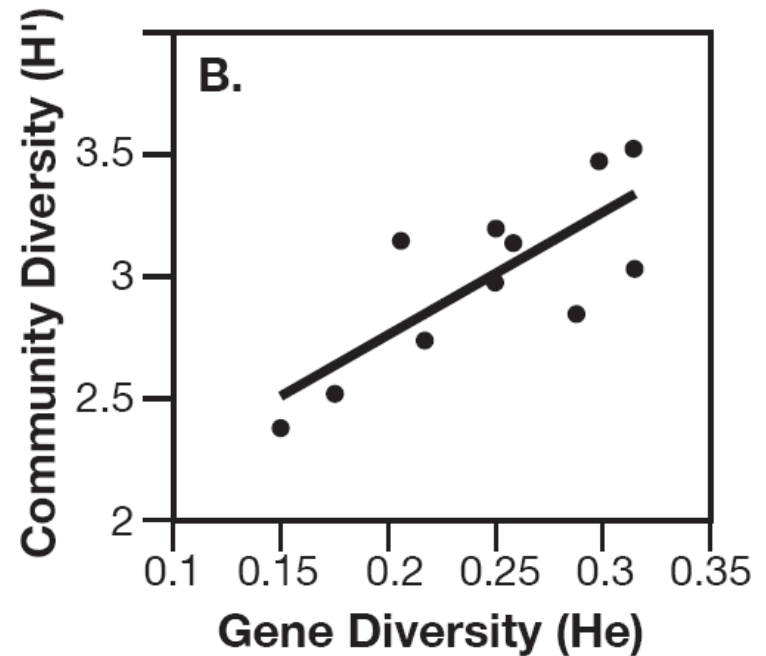


The relative fitness of different mite genotypes may covary with the genotype of their cottonwood host



Evans and Shuster, Unpublished Data

Genetic variation in cottonwoods influences arthropod communities in the wild and in common gardens



Whitham et al. 2006 *Nature Reviews Genetics*

Three Points:

- ✓ 1. Interspecific indirect genetic effects (IIGEs) *can* occur between plants and arthropods.
 2. A genetic basis arthropod community phenotype on cottonwood is measurable as H^2_C .
 3. Significant H^2_C indicates that selection community-level selection has occurred; community evolution is likely underway.

Two Possible Outcomes of IIGEs:

1. Community-level selection.
2. Phenotypic covariance among genetically related communities.



Community-Level Selection via IIGEs

Selection occurs *within a community context*.

Individual relative fitness *depends on* the genetic and demographic composition of its *community*.

The community *need not* have fitness such that differential extinction and proliferation of communities occurs.

(e.g., Wilson 1997)





Phenotypic Covariance Among Communities via IIGEs

Similar IIGEs are expected to produce phenotypically *similar* communities.

Hypothesis: If genetic interactions have *no* fitness effects,

no differences will exist in the composition of arthropod communities within or among cottonwood genotypes.

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.



A Test: Arthropod Communities on Cottonwood Clonal Replicates

We examined communities on 20 RFLP-confirmed tree genotypes within 4 tree crosstypes (Fremont, F1, BC, Narrowleaf) in a common garden.

3-6 replicate clones per genotype
($N_{\text{trees}} = 79$).





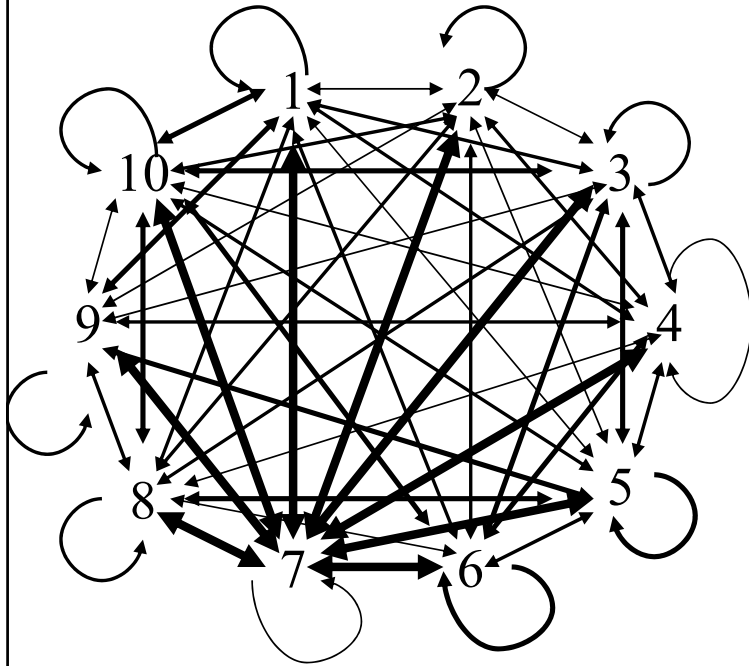
We Censused

The leaf modifying
arthropod community
14 species in 5 orders and
7 families

We Summarized

The number and type of
arthropods comprising
communities using non-
metric multidimensional
scaling (NMDS)

NMDS



Common and rare arthropod species are treated equally by NMDS, so observed score values represent *community-wide patterns*.

Captures the *phenotypic outcome* of trait interactions among cottonwoods and arthropods;
each community = a single NMDS score

Each NMDS score identifies a *community phenotype* for each clonal replicate within each tree genotype, but provides no specific information on the genetic basis for that score.

Three Analyses of Community Phenotype With Increasing Genetic Resolution

1. Line cross/joint scaling analysis of the effect of cross type
2. Nested ANOVA with genotype nested within cross type
3. 1-way ANOVA of genotype for each of the 4 cross types.

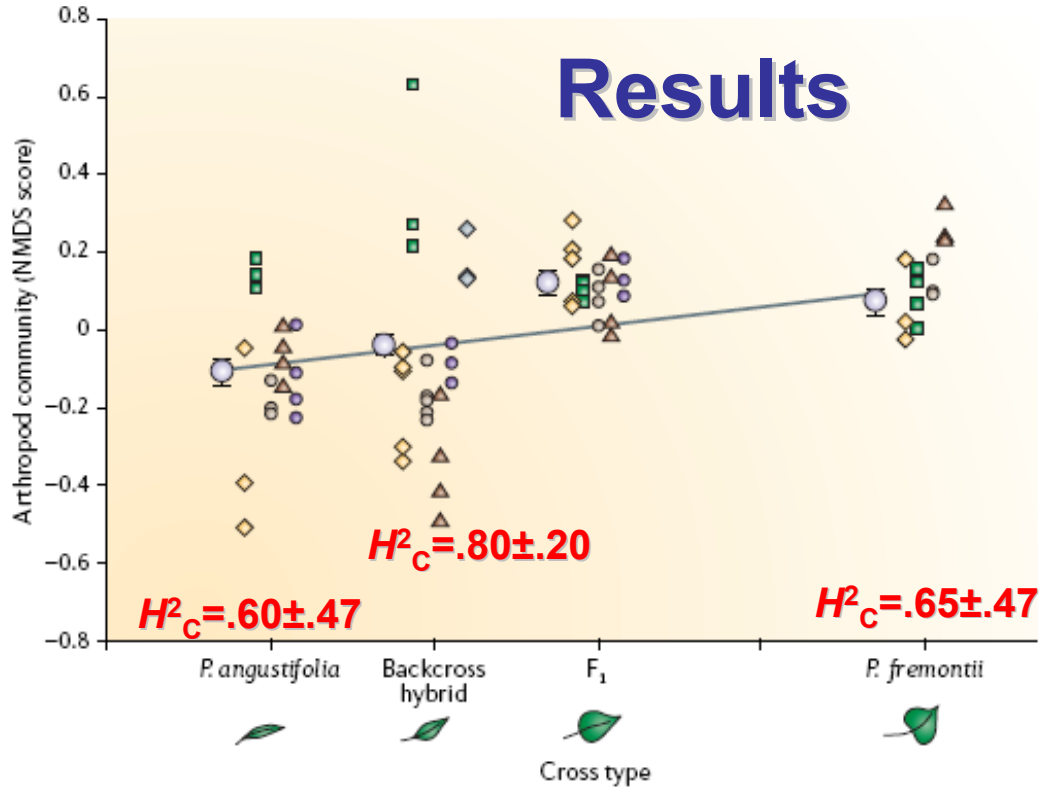
This Sequence Allowed Us To Determine:

Whether within- or between-species comparisons accounted for more of the total variation in community phenotype

The extent to which our inferences from this system may apply to other systems.

Whether estimates of H^2_C are possible and meaningful.

Results



Line cross/joint scaling analysis:

Non-significant additive and dominant effects between the two cottonwood species
Broad-sense heritability, H^2_c :
 $(R^2 = 1.69, df = 12, p = 0.143)$

For each parental type and for backcross hybrids was significant;
Nested-ANOVA:
 only H^2_c on F1 hybrids
 ~3X more variation in arthropod community phenotype explained by

Source	DF	SS	MS	F	Pr > F
Cross type	3	0.604	0.202	10.184	<.0001
Genotype(cross)	16	2.192	0.137	6.926	<.0001
Error	59	0.162	0.003		
Total	78	3.964			

Genetic variation within host plant species explained more variation in community phenotype than genetic variation between host plant species.

tree genotype within cross type (57%)
 than by
 tree cross type (19%).

Three Points:

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✓ 2. A genetic basis for arthropod community phenotype on cottonwood *is measurable* as H^2_C .

3. Significant H^2_C indicates that community-level selection has occurred; community evolution is likely underway.

The Basis for H^2_C

H^2_C is proportional to the product of:

the *broad sense heritability of the tree trait* used to identify genetically similar communities, θ_j ,

and the *intensity of community-level selection*, γ ,

relative to total selection in each ecological context, $(\gamma + E_n)$.

$$H^2_C \propto H^2_{\theta} \frac{\gamma}{\gamma + E_n}$$

Estimates of H^2_c

Quantify *more* than just the heritability of the tree trait.

They include the phenotypic effects of individual-level, *as well as* community-level selection,

$$H^2_c \propto H^2_\theta \frac{\gamma}{\gamma + E_n}$$

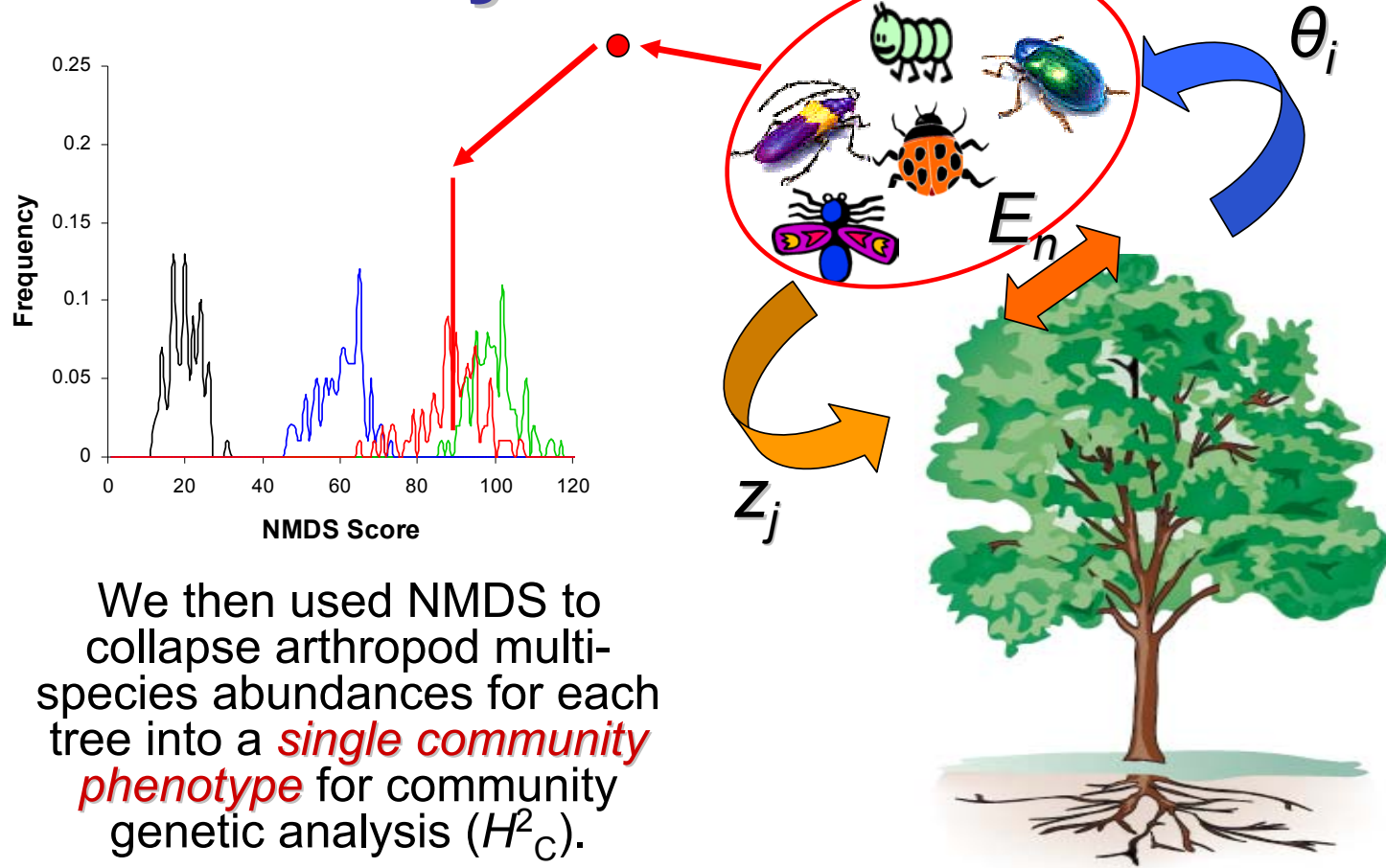
Can Simulated IGEs Produce Distinct Communities?



We modeled *synthetic communities* in which the number, intensity and fitness consequences of the IGEs were known.

We created synthetic trees in which a *single trait* influencing plant phytochemistry, θ_i , varied among tree genotypes and cross types.

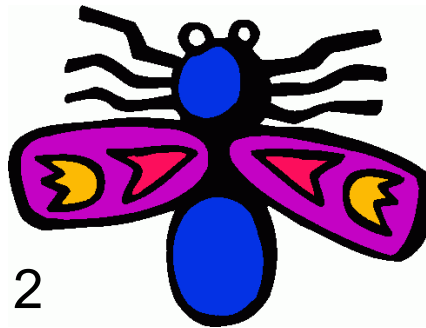
Synthetic Arthropods Sampled Synthetic Trees



We then used NMDS to collapse arthropod multi-species abundances for each tree into a *single community phenotype* for community genetic analysis (H^2_C).

Phytochemical Trait Expression

$$\theta_i = a_1 + a_2 + e_\theta$$

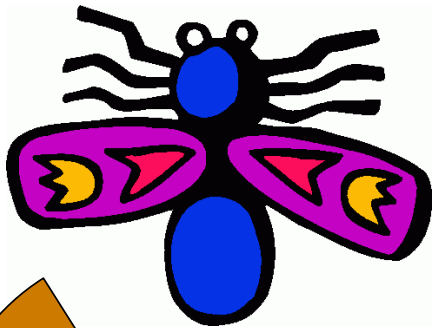


Was controlled by 2 alleles at a single locus

where a_1 was the additive effect of an allele on chromosome 1, a_2 was the additive effect of an allele on chromosome 2, e_θ represented random environmental effects; there was no dominance.



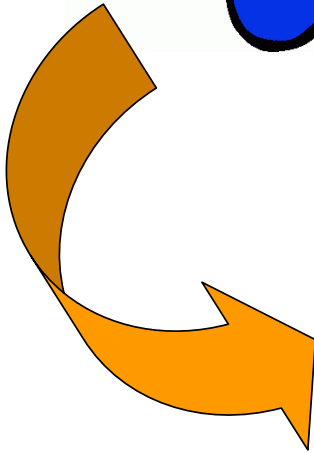
Arthropod Trait Expression



$$z_j = b_1 + b_2 + e_z$$

Was also controlled
by 2 alleles at a
single locus

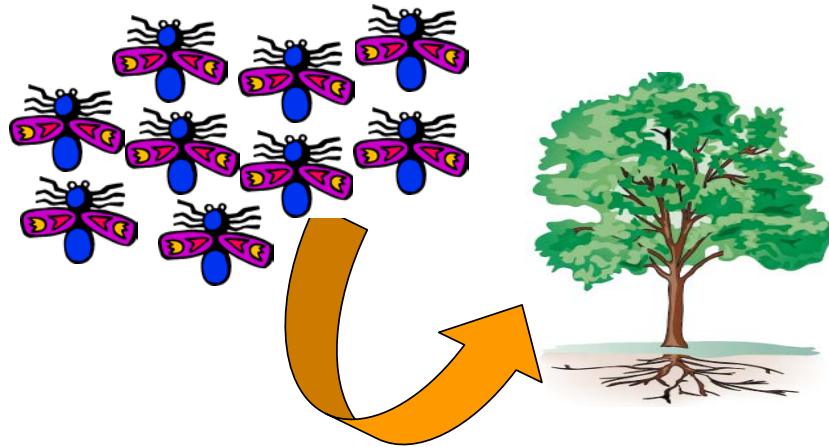
where b_1 was the additive
effect of an allele on
chromosome 1, b_2 was
the additive effect of an
allele on chromosome 2
and e_z represented
random environmental
effects.



The j -th Arthropod Phenotype on the i -th Cottonwood Tree

$$\bar{z}_{ij} = 2p_j^2 D_j + 2p_j(1-p_j)(C_j + D_j) + 2(1-p_j)^2 C_j$$

Was determined by the frequencies of the 2 alleles for each j -th arthropod species, C_j and D_j , with p_j as the population frequency of D_j .



Joint Changes in Arthropod Populations



$$\frac{d\bar{z}_{ij}}{dt} = \frac{\sigma_{G_{ij}}^2}{\sigma_{z_{ij}}^2} \gamma (\theta_i - \bar{z}_{ij}),$$



$$\frac{dn_{ij}}{dt} = n_{ij} \left[r \left(1 - \frac{n_{ij}}{K} \right) - \frac{\gamma}{2} \sigma_{z_{ij}}^2 - \frac{\gamma}{2} (\theta_i - \bar{z}_{ij})^2 \right]$$

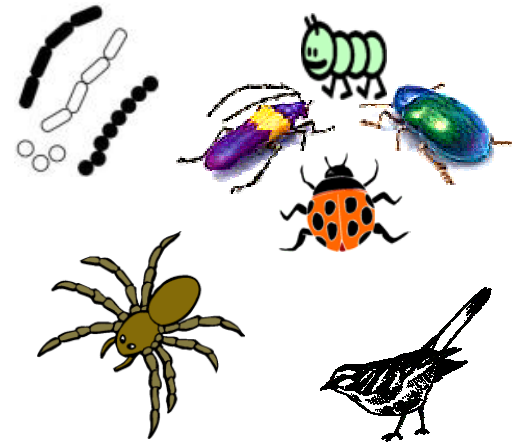
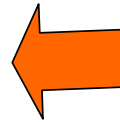
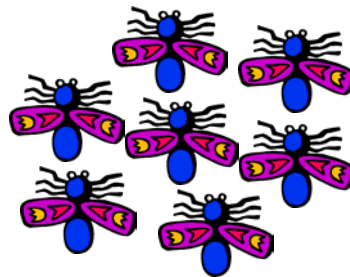
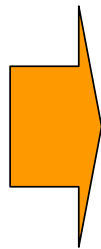
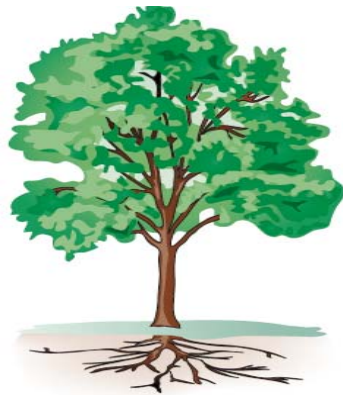
$$\frac{dp_{ij}}{dt} = \frac{d\bar{z}_{ij}}{dt} \frac{1}{2D_j - 2C_j}$$

c.f., Ronce & Kirkpatrick 2001

The Effects of Other Species

$$n_{ij}^* = K \left(1 - \frac{\gamma}{2} \sigma_{z,ij}^2 - \frac{\gamma}{2} \left(\theta_i - \bar{z}_{ij}^* \right)^2 \right) + E_{n_{ij}}$$

Depended on the relative magnitude of ecological interactions other than the tree on the population size of the j -th arthropod species, on the i -th tree, with E_n proportional to carrying capacity.



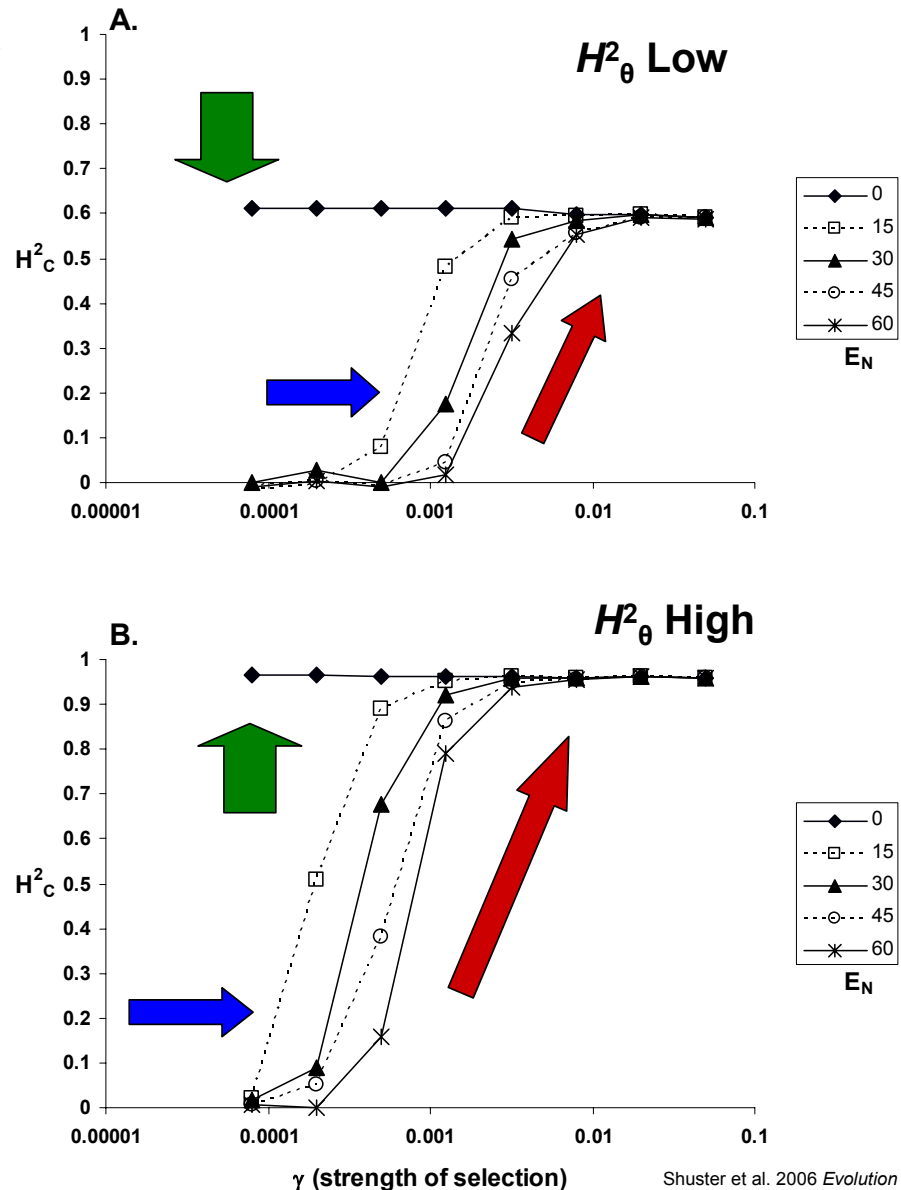
H^2_C : Effects of H^2_θ , γ and E_n

As selection (γ) *increased*, community heritability *increased*.

As ecological variation (E_n) *increased*, the rate of increase *declined*.

H^2_C *was* proportional to plant heritability (H^2_θ).

H^2_C *was lower* when plant heritability was lower (A) and *higher* when plant heritability was higher (B).



Three Points:

1. Interspecific indirect genetic effects (IIGEs) *can occur* between plants and arthropods.
2. A genetic basis for arthropod community phenotype cottonwood *is measurable* as H^2_C .
3. Significant estimates of H^2_C *do indicate* that community-level selection *has occurred*; community evolution is likely *underway*.

Common Gardens

**Replicated
clones and experimental
crosses map
ecologically
important traits and
quantify heritability.**



**Restoration at a former
Super Fund site**

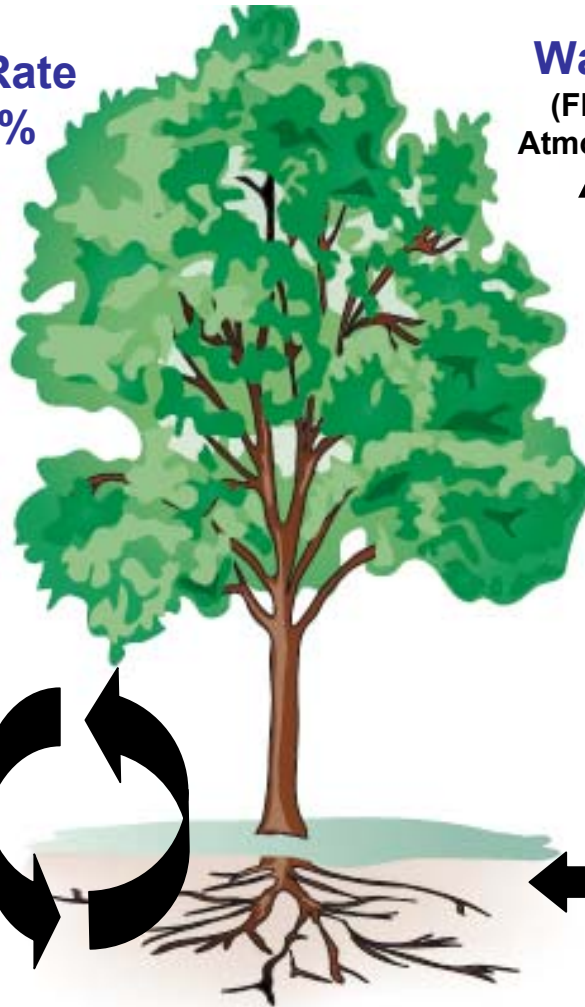


Plant Genetic Factors Account for ~50% of the Variation in Ecosystem Services

Plant Growth Rate

Constant 45%

(Productivity)
Lojewski et al.
unpub. data



Water Cycles 35-40%

(Fluxes from Soil to Plant to Atmosphere) Fischer et al. 2004
Oecologia

Biodiversity 43-78%

(Microorganisms, Herbivores, Birds) Wimp et al. 2004 Ecology Letters, Bangert et al. 2004 Conservation Biology, Shuster et al. 2006 Evolution, Bailey et al. Ecology Letters 2006, LeRoy et al. 2006 Ecology, Schweitzer et al. 2006 & unpub. data



Nutrient Cycles

34-65%

(Soil Fertility)
Schweitzer et al.
2004 Ecology Letters,
2005 Ecology, 2005
Oikos, LeRoy et al.
2006 Ecology



Belowground Carbon Storage & Root Production 77%

Fischer et al. 2006 Oecologia

Application in Restoration



Photo credit: BOR

A 40-acre common garden was planted with ~10,000 trees in 2005 to study the effects of tree genetic diversity on the diversity of the arthropod and microbial communities.



RECLAMATION
Managing Water in the West

Conservation Implications

There are evolutionary genetic reasons why *monocultures* decrease total species diversity.

Relative stability may depend on the strength and diversity of different IIGEs.



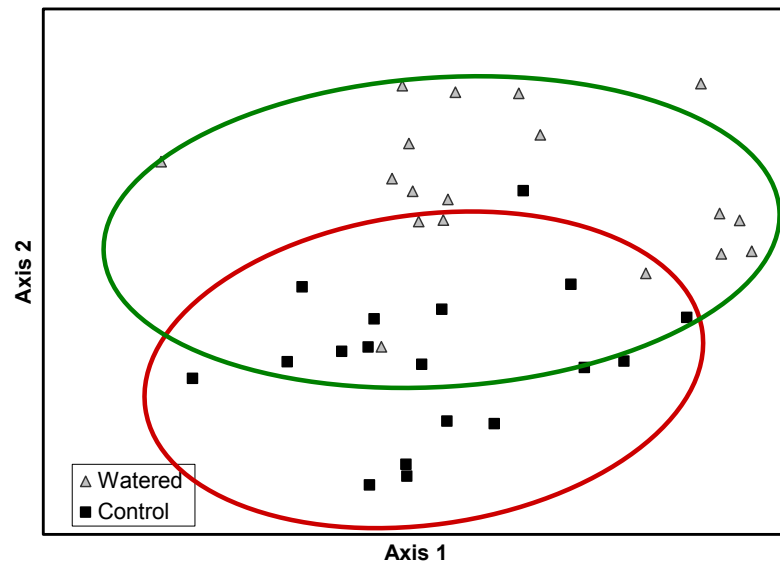
Conservation Implications

There are evolutionary genetic reasons why *Global Climate Change* can have far reaching consequences.

Drought in Arizona *has* significant effects on arthropod communities.



2003 Community Composition of Watered and Control Trees

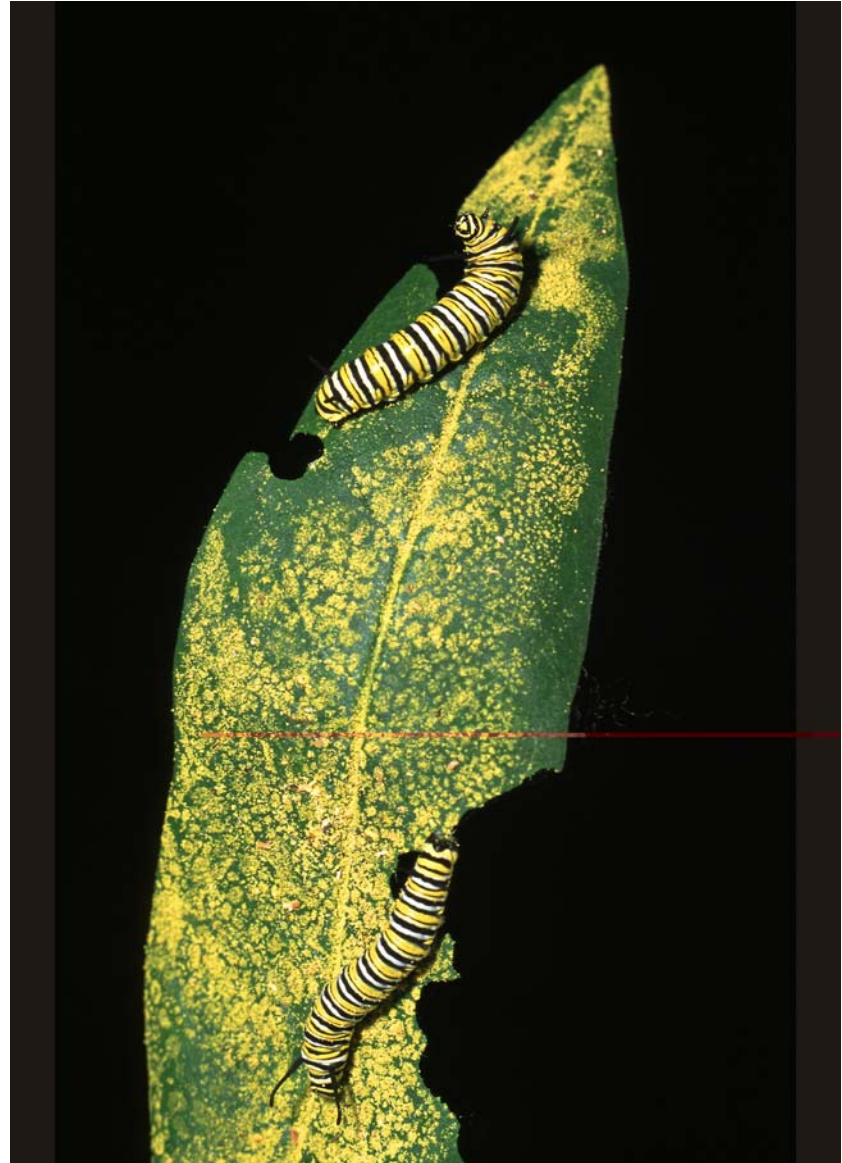


Scudder et al., 2005, Unpublished data

Conservation Implications

There are evolutionary genetic reasons why *Genetically Modified Organisms* must be introduced with care.

The ecological consequences of novel IIGEs may be difficult to predict.



Community and Ecosystem Phenotypes, and Heritability in Diverse Systems

Level of Investigation	System	Plant	Phenotypes Type	Heritability	Foundation Species
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Community

<i>Eucalyptus</i>	Tree	1	Unmeasured	Yes
<i>Oenothera</i>	Herb	1	Yes	No
<i>Pinus</i>	Tree	4	Unmeasured	Yes
<i>Populus</i>	Tree	1-3	Yes	Yes
<i>Quercus</i>	Tree	1	Unmeasured	Yes
<i>Salix</i>	Tree	1	Unmeasured	Yes
<i>Solidago</i>	Herb	1	Unmeasured	Yes

Ecosystem

<i>Metrosidero</i>	Tree	7	Unmeasured	Yes
<i>Populus</i>	Tree	5-7	Yes	Yes
<i>Quercus</i>	Tree	6,7	Unmeasured	Yes
<i>Solidago</i>	Herb	8	Unmeasured	Yes

Organism: 1-arthropods, 2-microbes and fungi, 3-vertebrates, 4-plants
 Process: 5-litter decomposition, 6-energy flow, 7-nutrient cycles, 8 productivity.

Whitham et al. 2006 Nature Reviews Genetics, plus new studies

Why Do We Need a Community Genetics Perspective?

1. Prevailing models of community organization and ecosystem dynamics **do not** include a genetic-based perspective (e.g., Hubbell's null model hypothesis).
2. Ignoring IIGEs may exclude a **significant component** of total selection on ecologically important traits.
3. A genetic-based framework places community and ecosystem ecology within an **evolutionary framework**.



Community & Ecosystem Genetics

Gery Allan – molecular systematics
Brad Blake – greenhouse manager
Aimee Classen – ecosystem dynamics
Eck Doerry – bio-informatics
Kevin Floate – insect ecology
Alicyn Gitlin – drought ecology
Steve Hart – ecosystem/soil ecology
Barbara Honchak – ecological genetics
Karla Kennedy – resotation ecology
Carri LeRoy – aquatic ecology
Eric Lonsdorf – genetic modeling
Becky Mueller – plant ecology
Jen Schweitzer – ecosystems
Steve Shuster – theoretical genetics
Richard Turek – statistics
Amy Whipple – ecological genetics
Todd Wojtowicz – microarthropods
Matt Zinkgraf – molecular ecology

Joe Bailey – community ecology
Bill Bridgeland – avian ecology
Ron Deckert – endophyte ecology
Luke Evans – population ecology
Robert Footitt – molecular systematics
Laura Hagenauer - biodiversity
Kris Haskins – mycorrhizal ecology
Paul Keim – microbial genetics
Zsuzsi Kovacs – mycorrhizal ecology
Rick Lindroth – chemical ecology
Jane Marks – aquatic ecology
Brad Potts – population genetics
Crescent Scudder – plant demography
Adrian Stone – insect communities
Talbot Trotter – dendrochronology
Tom Whitham – ecology
Stuart Wooley – phytochemistry

Randy Bangert – biogeography
Sam Chapman – nutrient cycling
Steve DiFazio – molecular ecology
Dylan Fischer – ecophysiology
Catherine Gehring – microbial ecology
Allen Haden – aquatic ecology
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Nathan Lojewski – productivity
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Brian Rehill – chemical ecology
David Smith – spatial genetics
Chris Sthultz – population ecology
Pam Weisenhorn – nutrient cycling
Gina Wimp – community ecology
Scott Woolbright - molecular genetics

GO and NGO collaborators

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Russ Lawrence – Utah Dept. of Natural Resources



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Gregg Garnett – Bureau of Reclamation
Mary McKinley – Ogden Nature Center

