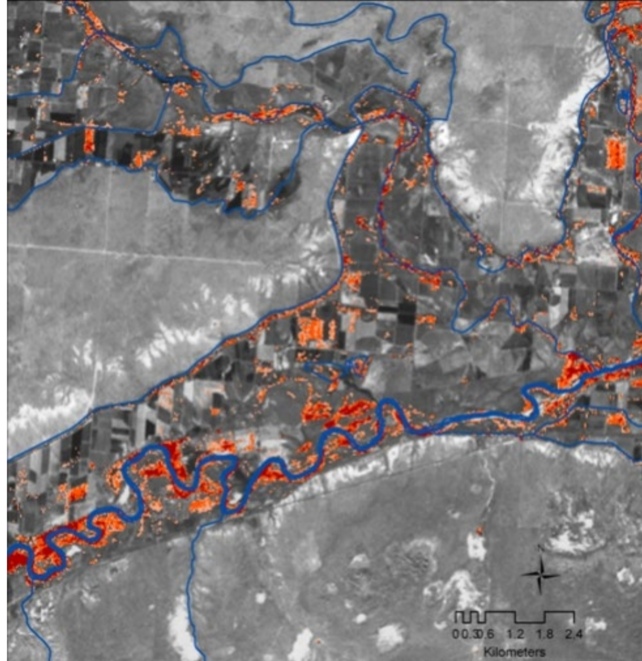
PLANT OF THE DAY!

•Tamarix (salt cedar)
• 50-60 species
•Family Tamaricaceae
•native to dry areas of Eurasia and Africa.

•Introduced to North America as ornamental shrub in 19th century
•Planted extensively during great depression to prevent soil erosion

•Second worst invasive species in USA
•Colonizes riparian habitats, displacing native vegetation and consume precious water resources

•Most common invasive in USA is a **hybrid** of two species that do not grow in the same areas of Asia




Hybridization and
Reinforcement

Questions

How frequent is hybridization in plants?

What is the role of hybridization in plant evolution?

“. . . in such [hybridizing] populations, the raw material for evolution brought in by introgression must greatly exceed the new genes produced directly by mutation.”

Anderson (1949, p. 102)

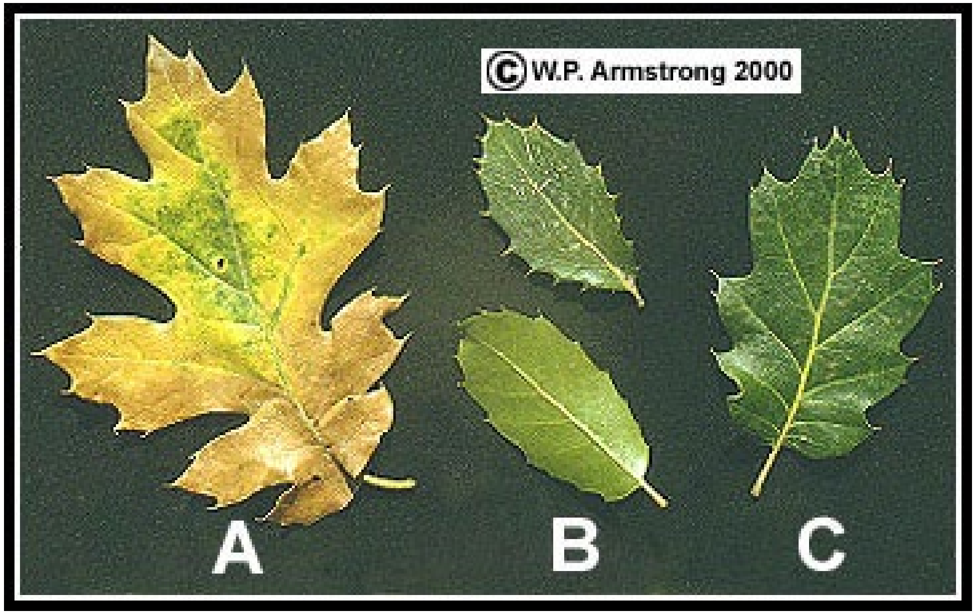
“The major point to be stressed with respect to the role of hybrids in diversity is that they are intermediate. . . For this reason, the ultimate contributions to overall diversity made by hybrids must be small or negligible.”

Wagner (1969, p. 785)

Terms

What is hybridization?

mating between different varieties or species



Hybrid Oaks

What is Introgression?

the movement of genes from one variety or species to another by repeated backcrossing

Introgression

How frequent is hybridization?

Table 1
Summary statistics on the recorded prevalence of natural hybridization in plants.

Region	Families			Genera			Nonhybrid Species	Hybrids	
	Number	Number with hybrids	% With Hybrids	Number	Number with hybrids	% With Hybrids	Number	Number	Number per nonhybrid species
California, USA	171	51	29.8	1252	126	10.1	5996	389	0.065
Europe	184	58	31.5	1529	196	12.8	12,255	1340	0.109
British Isles	162	63	38.9	947	183	19.3	3009	770	0.256
Great Plains, USA	159	33	20.8	842	64	7.6	2856	153	0.054
Hawaii	164	40	24.4	715	59	8.3	1997	210	0.105
Intermountain West, USA[a]	110	33	30.0	742	86	11.6	3179	204	0.064
New England, USA	177	37	20.9	1018	54	5.3	3613	136	0.038
Victoria, Australia	177	37	20.9	1054	83	7.9	4035	235	0.058
Global totals	1304	352	27.0	8099	851	10.5	36,940	3437	0.093
Global totals (unique taxa)	282	114	40.4	3212	521	16.2	[b]	[b]	[b]

[a] Flora not yet complete; numbers reflect taxa in the published volumes only.
[b] Because data were collected at the generic level, the numbers of unique nonhybrid species and hybrids are not estimated.

Whitney et al. 2010

What are the evolutionary consequences of hybridization?

- Merger of species (destructive role)
- Stable hybrid zones, balanced by selection against hybrids and gene flow into the zone (neutral role)
- The origin and transfer of adaptations (creative role)
- Creation of novel or extreme phenotypes (creative role)
- The reinforcement of reproductive barriers (creative role)
- The birth of new hybrid lineages (creative role)

Merger of species (destructive role)

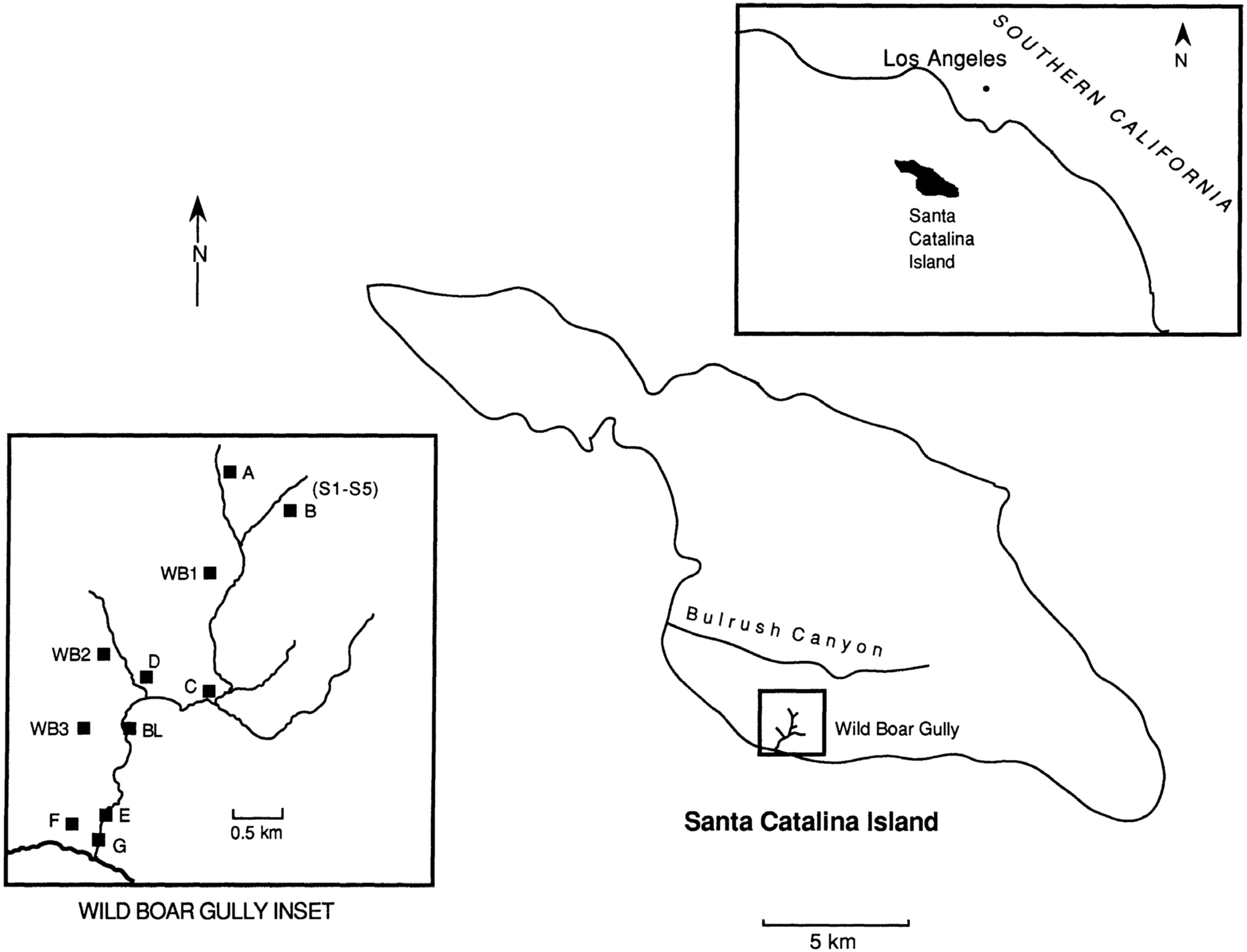
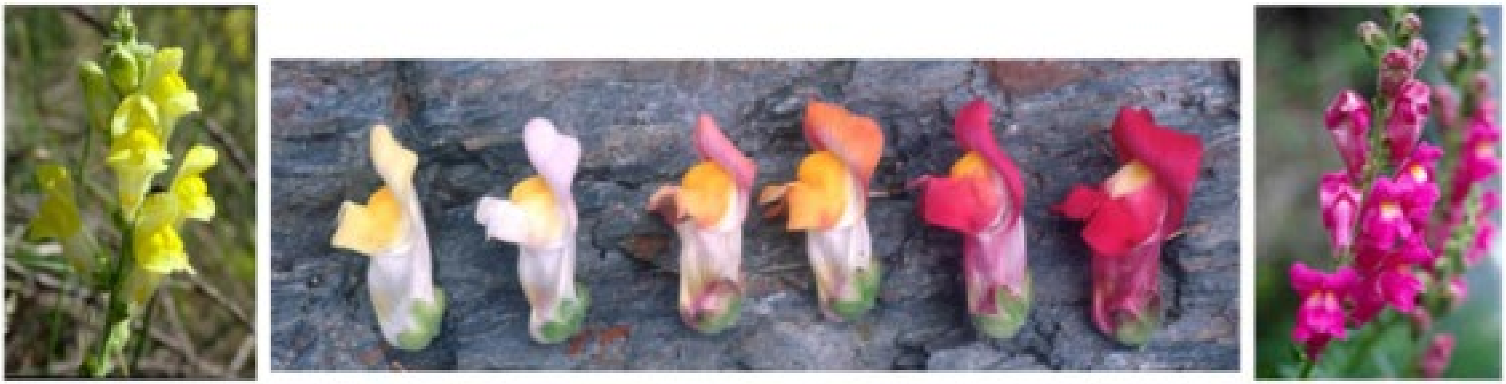
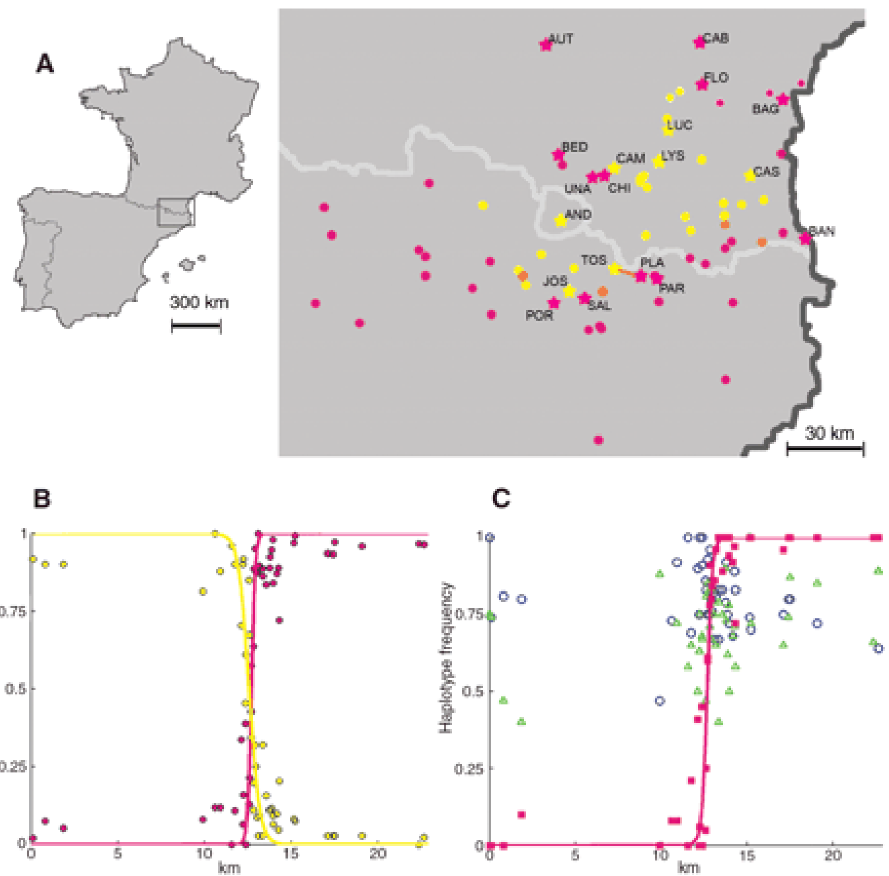


Figure 1. Map of Santa Catalina Island showing distribution of Cercocarpus *in Wild Boar Gully (map has been updated and corrected from Rieseberg et al. 1989). Trees* A-D, WB1-WB2 *are true* C. traskiae; *trees* E-G, BL, WB3 *and seedlings* S1-S5 *are hybrids between* C. traskiae *and* C. betuloides *var.* blancheae.

Stable hybrid zones, balanced by selection against hybrids and gene flow into the zone (neutral role)

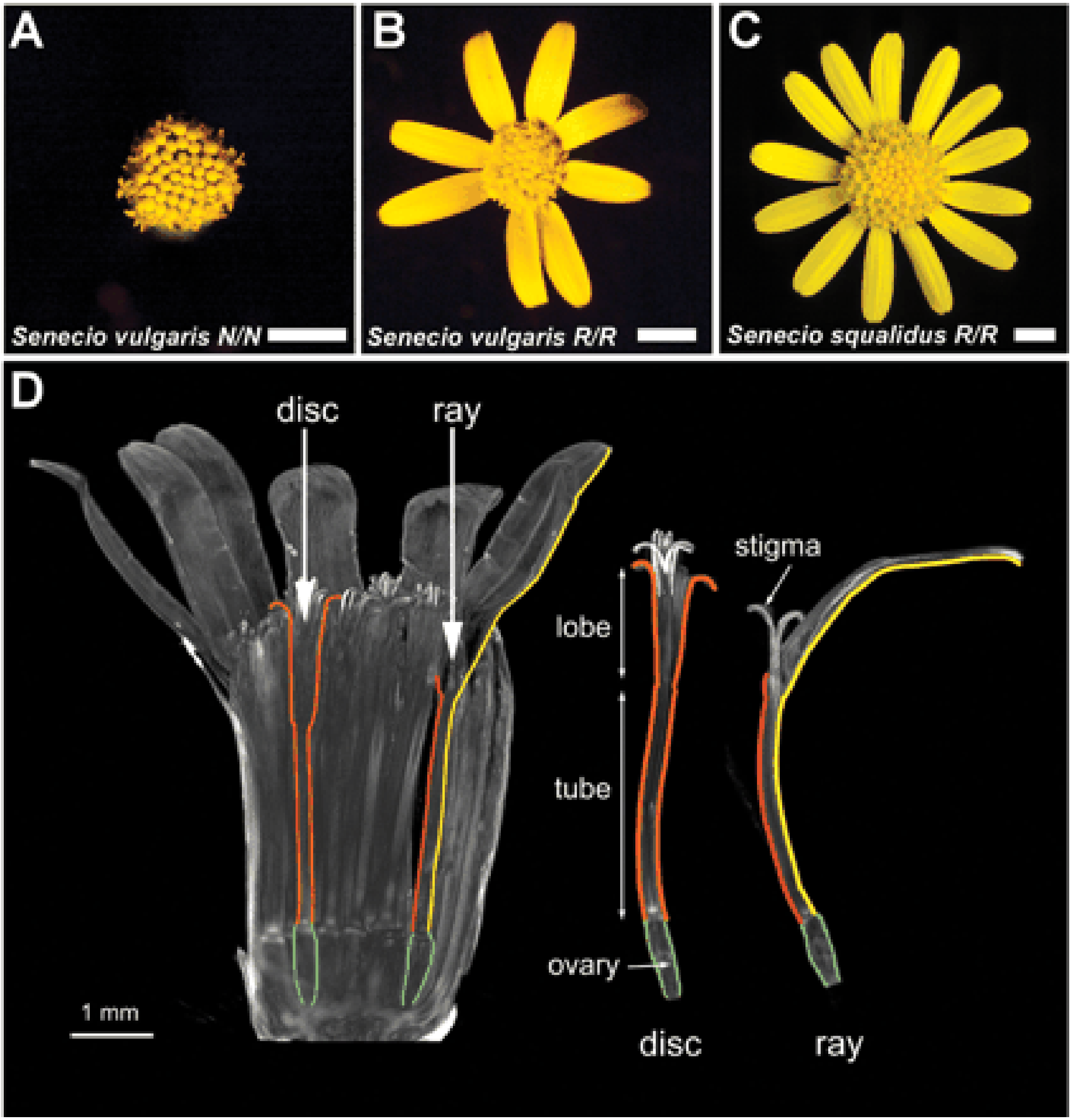


Steep clines indicate strong selection against hybrids (Whibley et al. 2006)



The origin and transfer of adaptations (creative role)

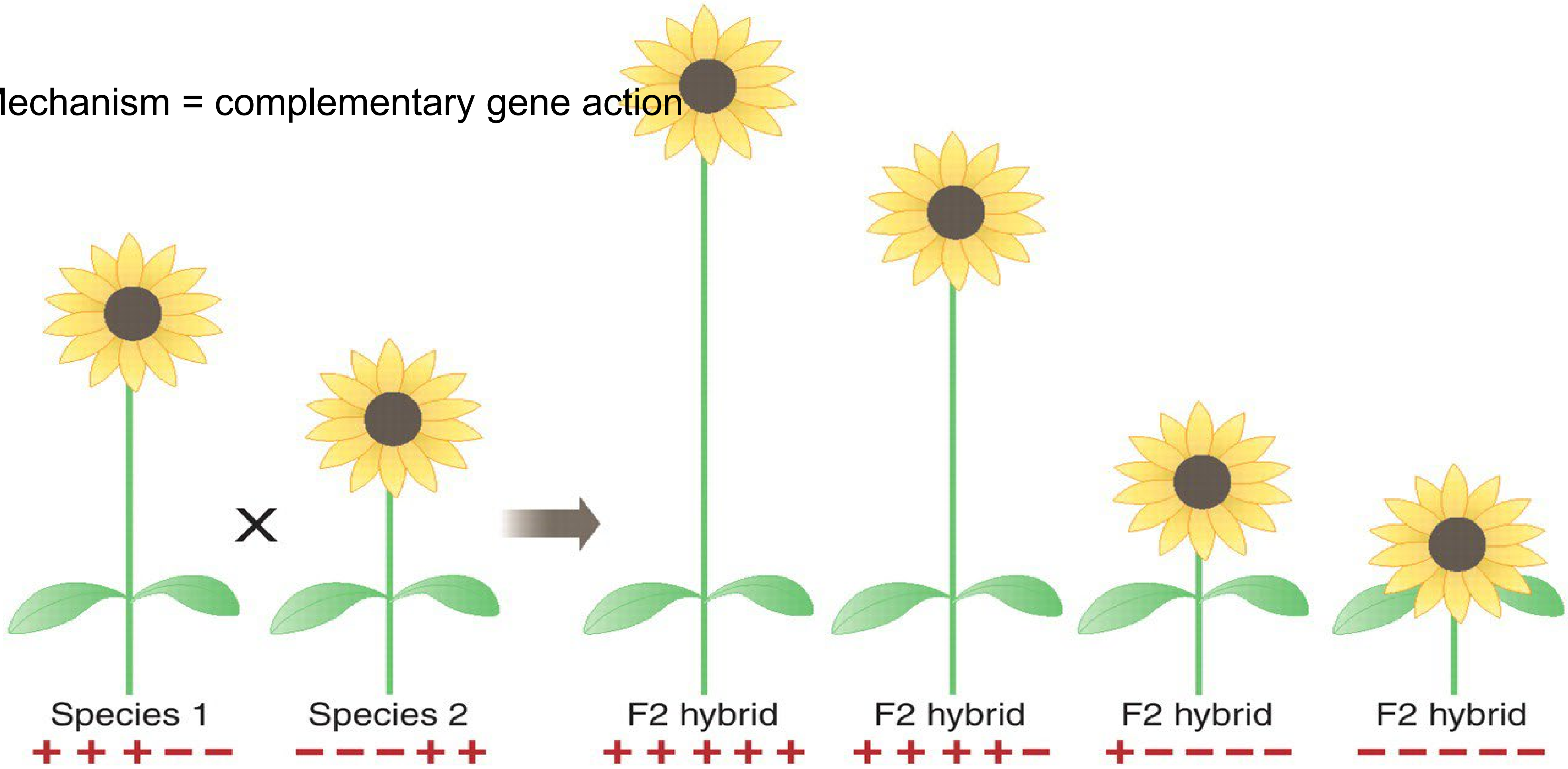
Ray flowers and outcrossing regained through introgression in Senecio (Kim et al. 2008)



How does hybridization create novel or extreme phenotypes?

•Natural populations of organisms often contain cryptic variation that cannot be predicted from the phenotype of the population.
•Cryptic variation is released in crosses through the expression of extreme or “<u>transgressive</u>” phenotypes

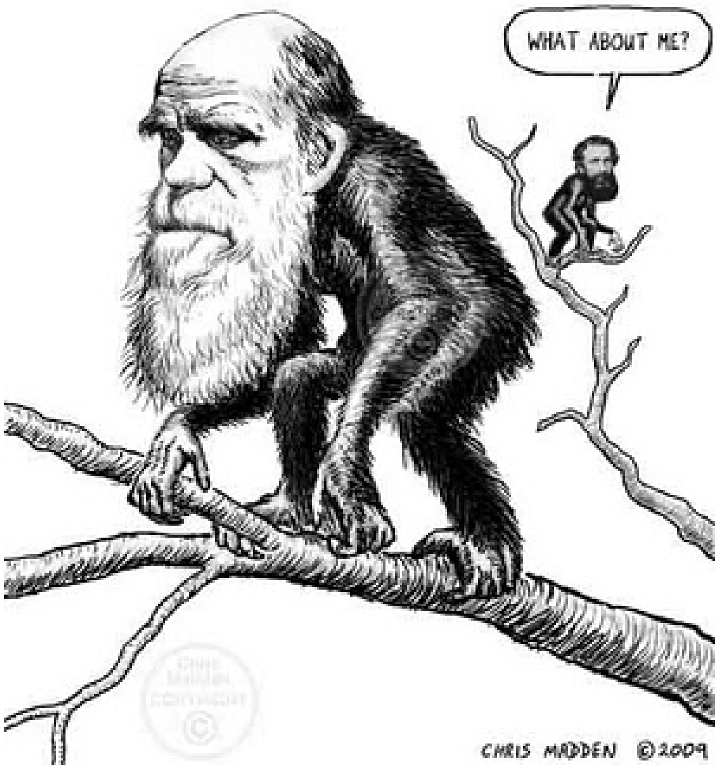
Mechanism = complementary gene action

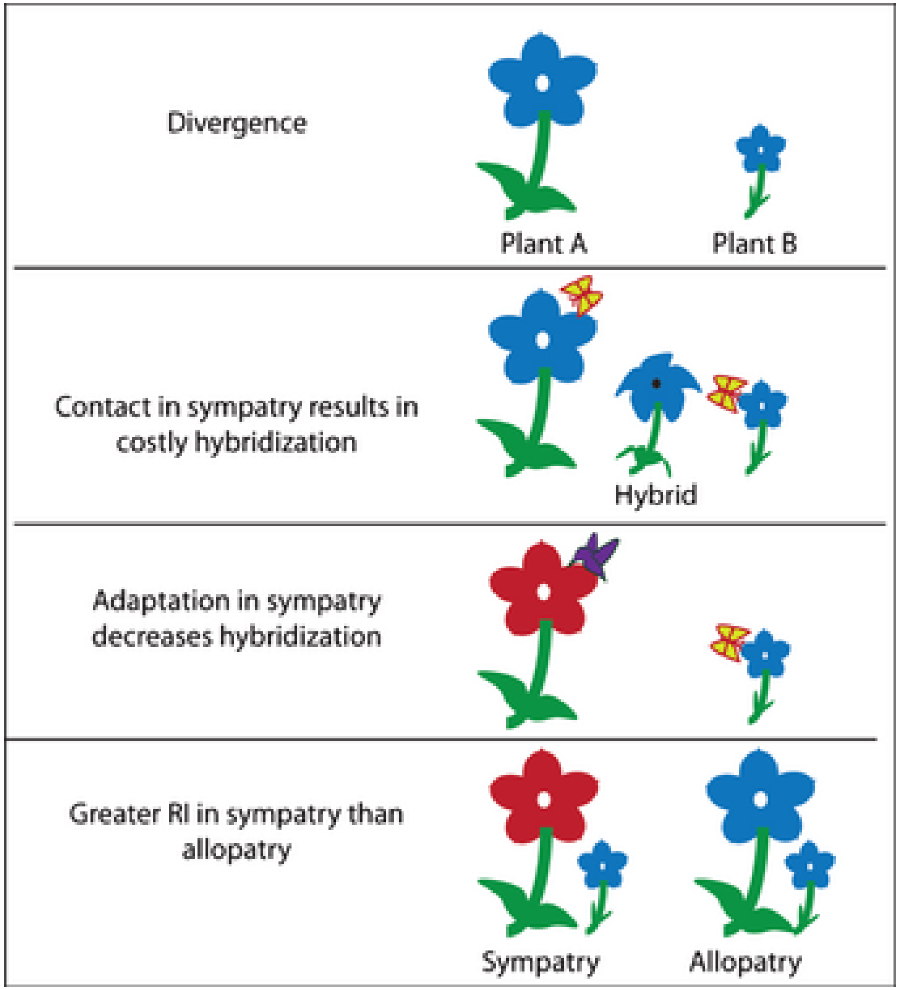


The reinforcement of reproductive barriers (creative role)

Darwin - reproductive barriers byproduct of adaptation

Wallace - selection against hybrids favored development of reproductive barriers





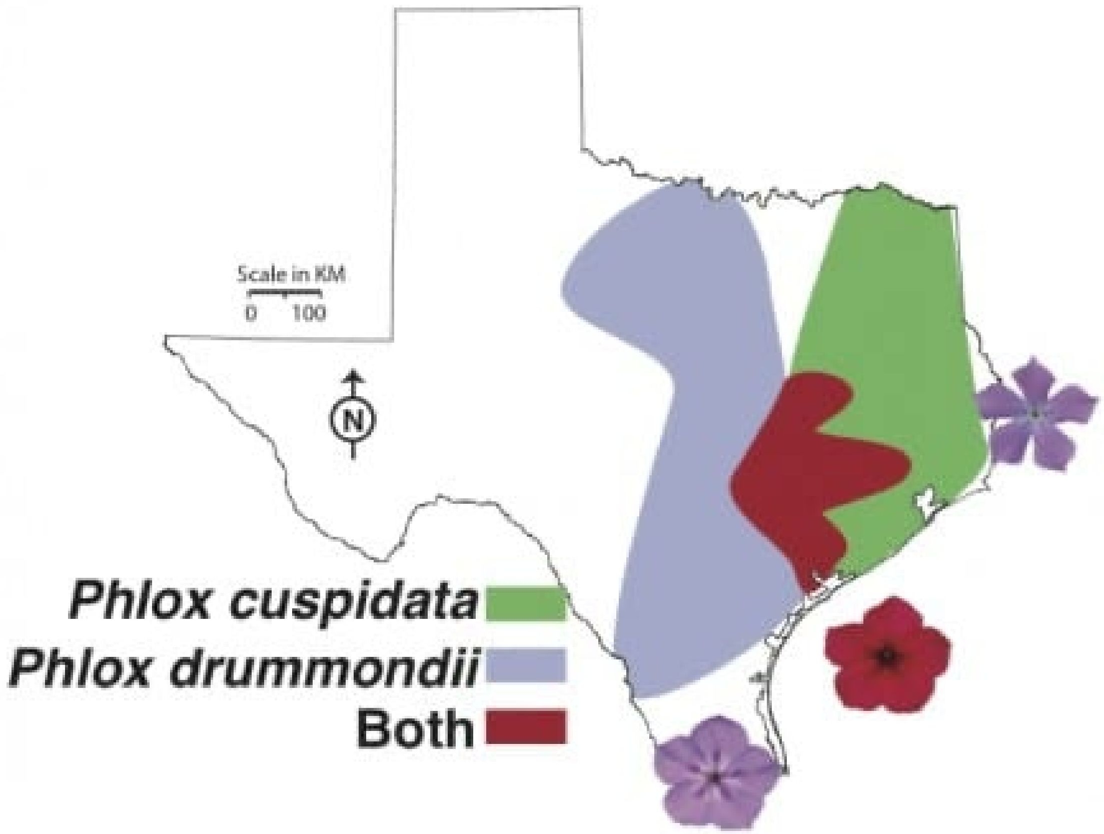
New Phytologist
Volume 197, Issue 4, pages 1095-1103, 16 JAN 2013 DOI: 10.1111/nph.12119
http://onlinelibrary.wiley.com/doi/10.1111/nph.12119/full#nph12119-fig-0001

Reinforcement in Phlox

Phlox drummondii and *Phlox cuspidata* are annual herbs native to east and central Texas.

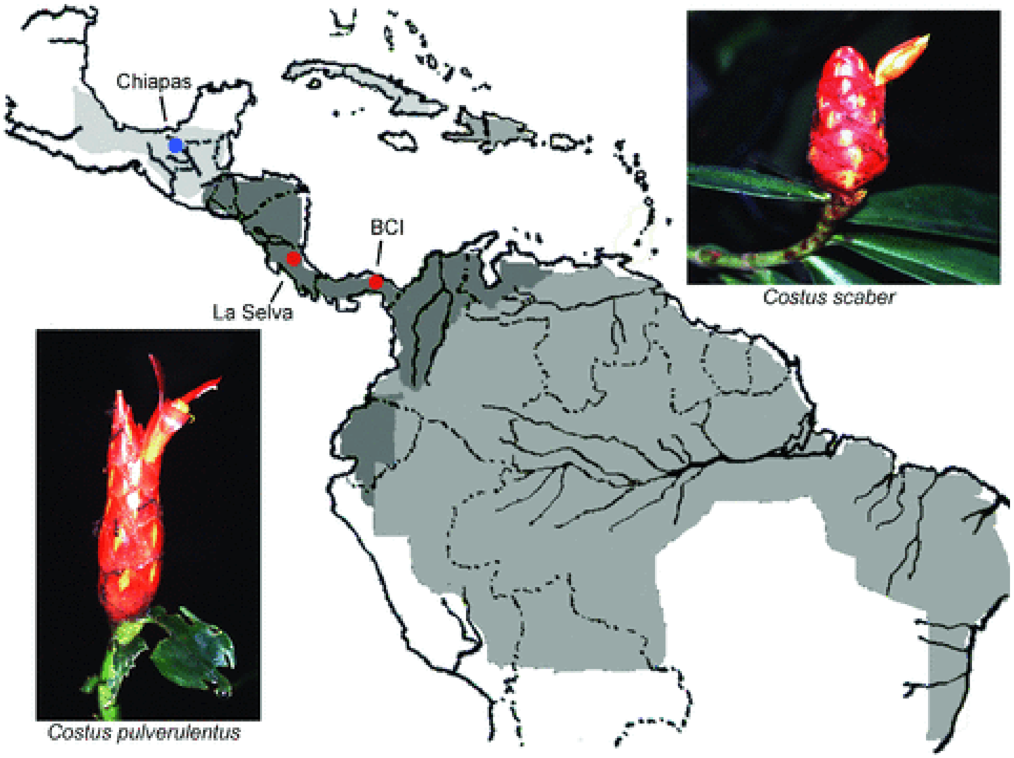
Throughout most of their ranges, they have light-blue flowers characteristic of the Phlox clade.

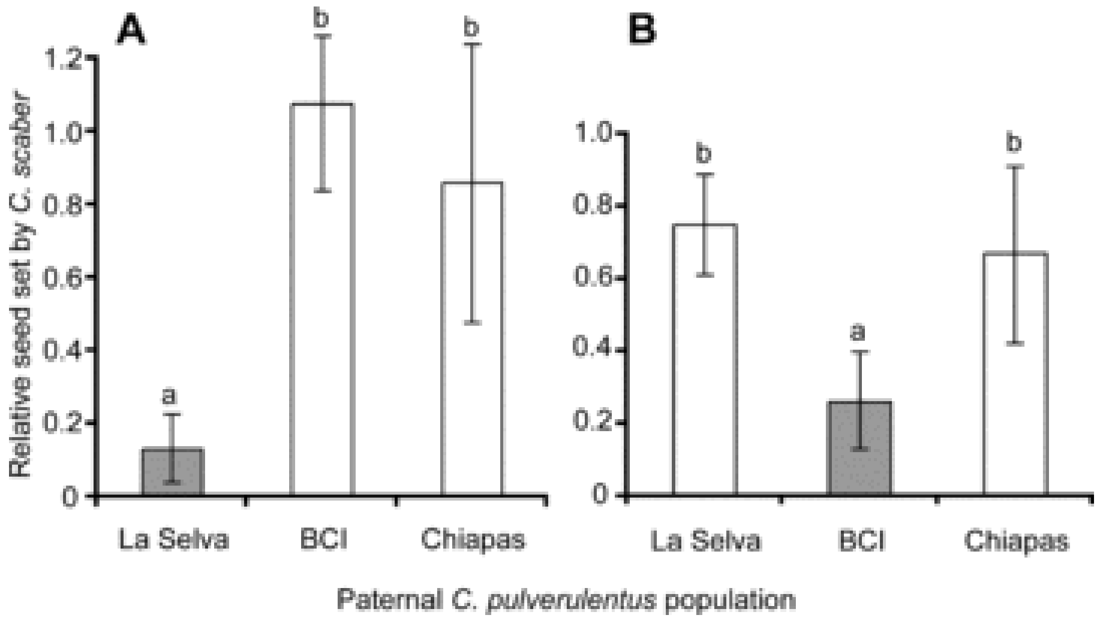
Where these two species co-occur *P. drummondii* has dark-red flowers



Robin Hopkins

Reinforcement in Costa



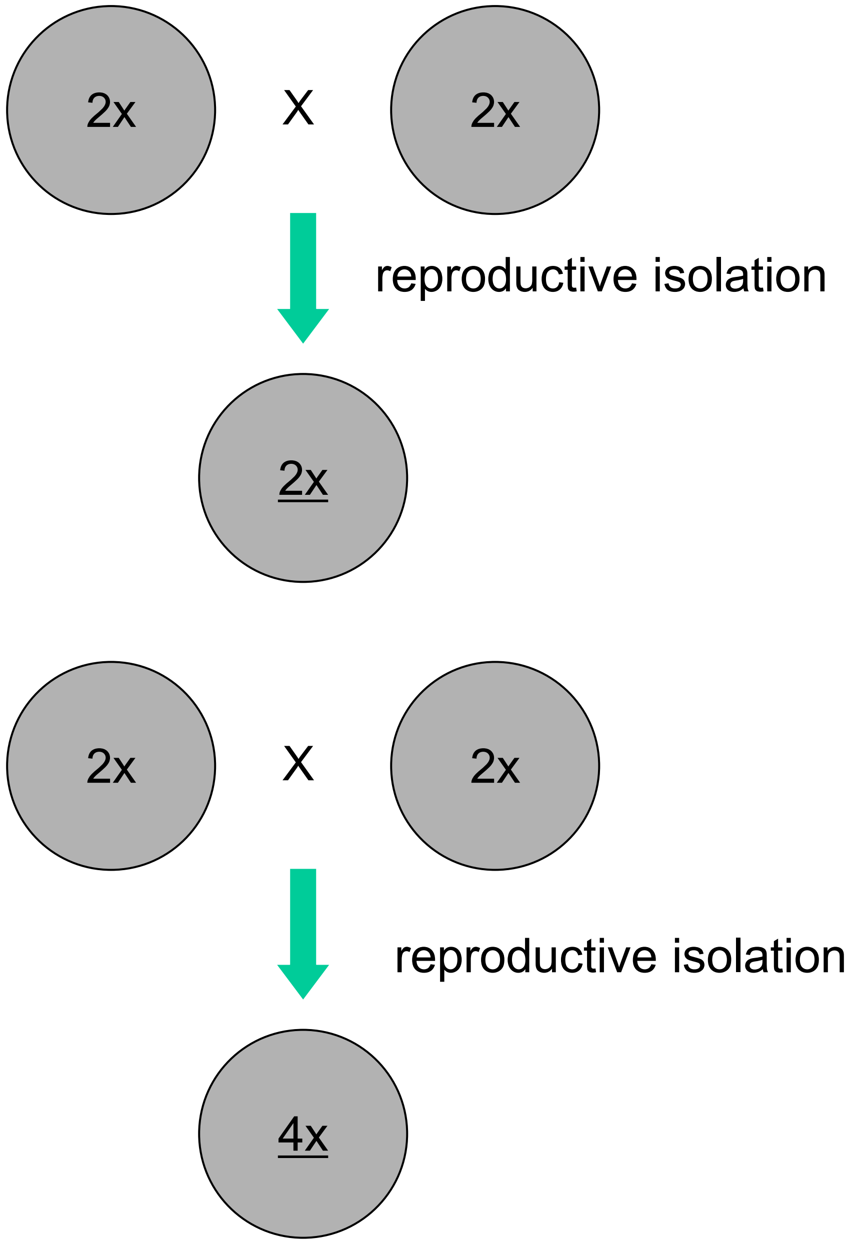


Ranges of *C. pulverulentus* and *C. scaber, which* are sympatric in Central America (dark gray), but allopatric elsewhere (*C. pulverulentus*, light gray; *C. scaber*, medium gray).

Mean relative seed set for *C. scaber* from (A) La Selva and (B) BCI. Shaded bars indicate locally sympatric pairings

Kay and Schemske (*Evolution* 2008)

Kinds of Hybrid Speciation



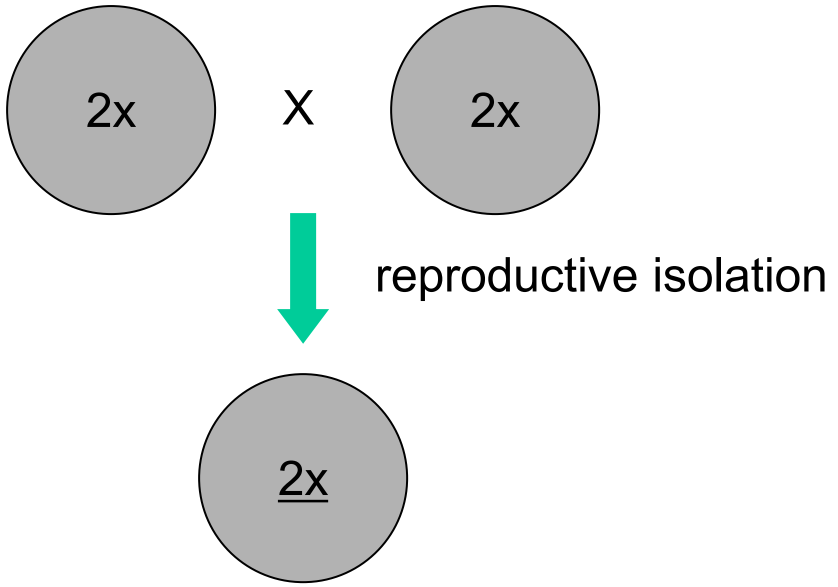
Homoploid Hybrid Speciation

Which mode of hybrid speciation is more common? Why?

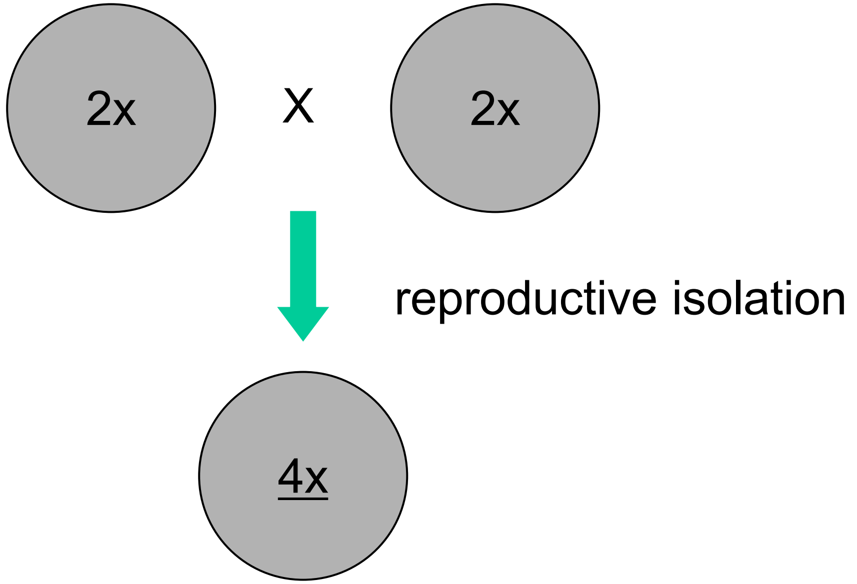
Polyploid Hybrid Speciation
(Allopolyploidy)

Kinds of Hybrid Speciation

Homoploid Hybrid Speciation
•Rare
•Reproductive isolation difficult to achieve



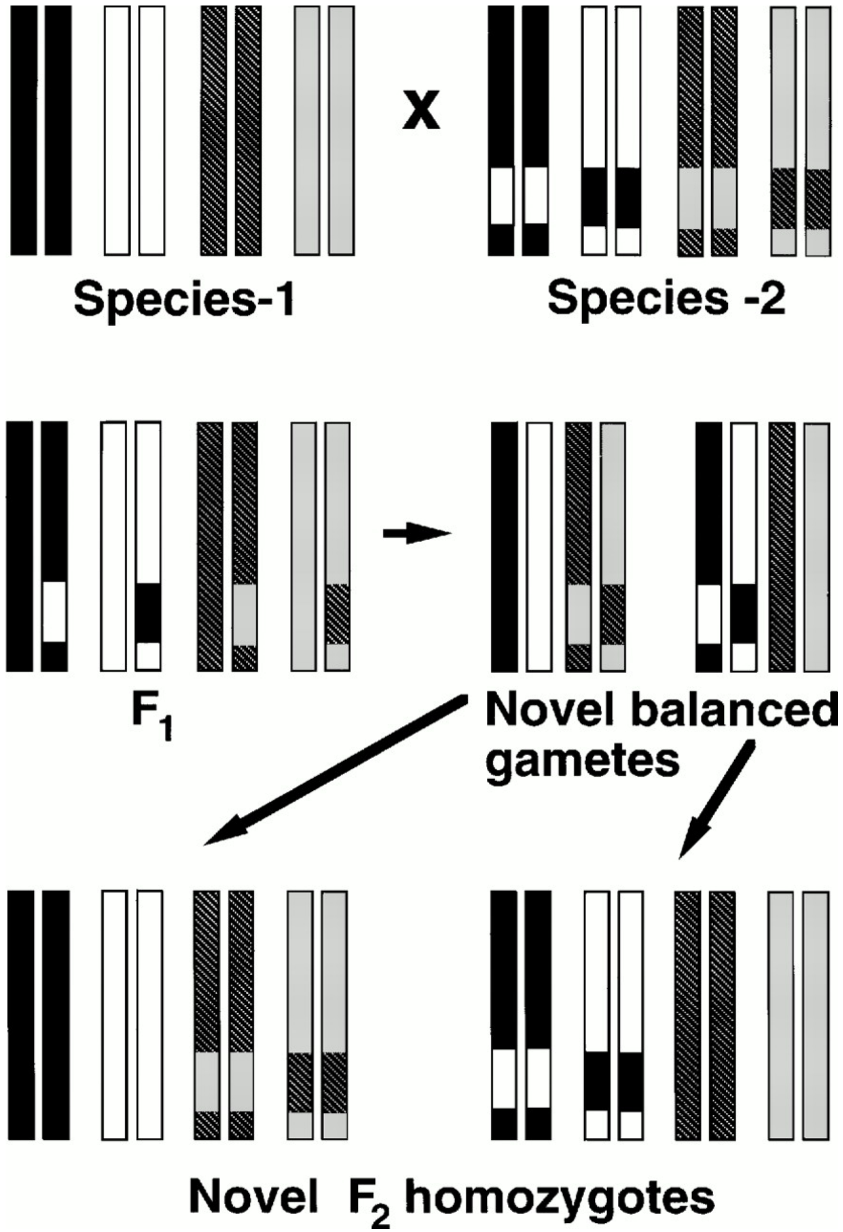
Polyploid Hybrid Speciation
(Allopolyploidy)
•Common
•Reproductive isolation byproduct of genome doubling



Model for Homoploid Hybrid Speciation

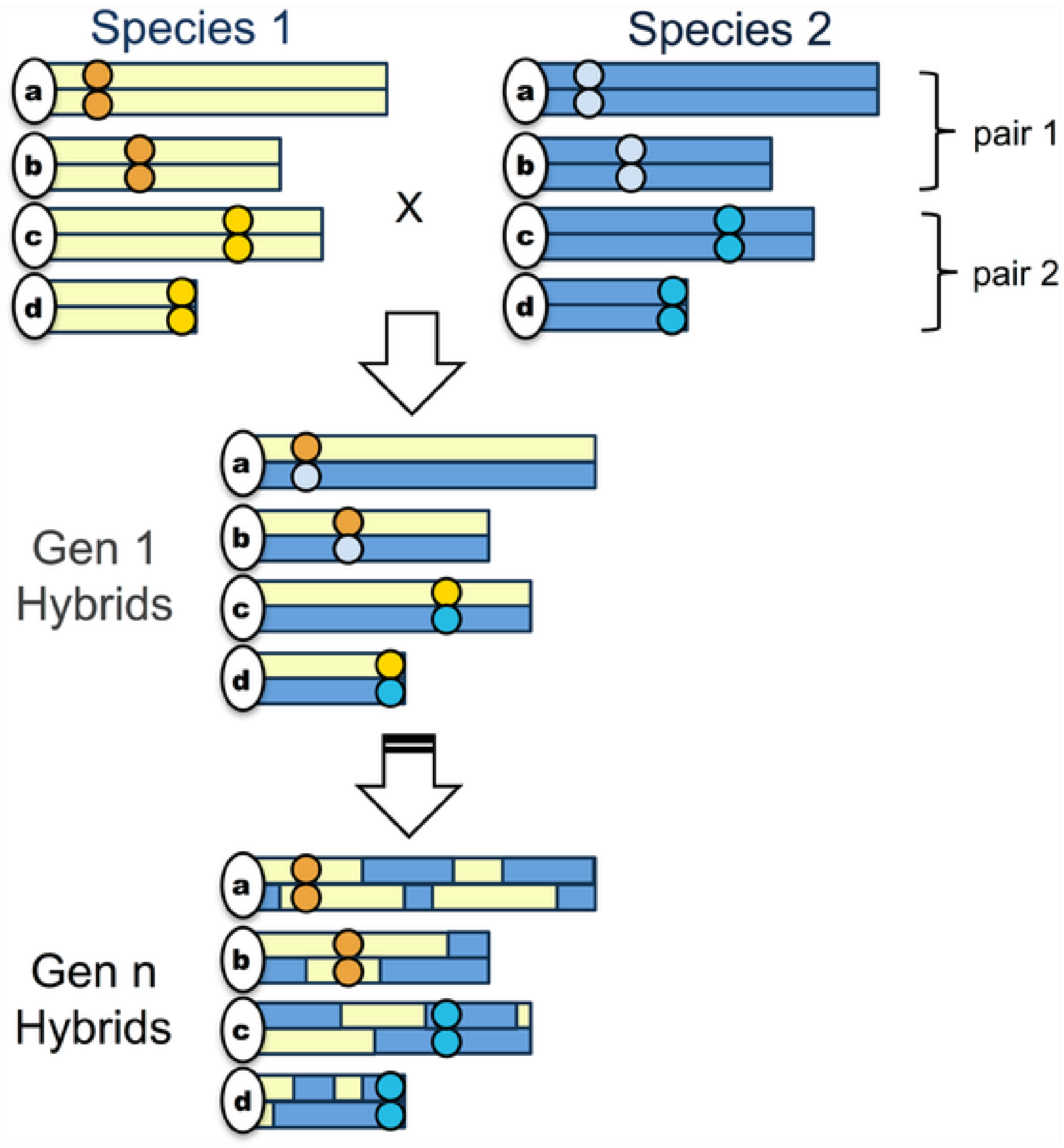
- Interspecific hybridization
- Fertility / viability selection
- Stabilization of fertile & viable hybrid segregates
- Reproductive isolation facilitated by
  - karyotypic divergence (recombinational model)
  - hybrid trait causes ecological divergence
  - hybrid trait causes assortative mating
  - spatial isolation

Recombinational Model



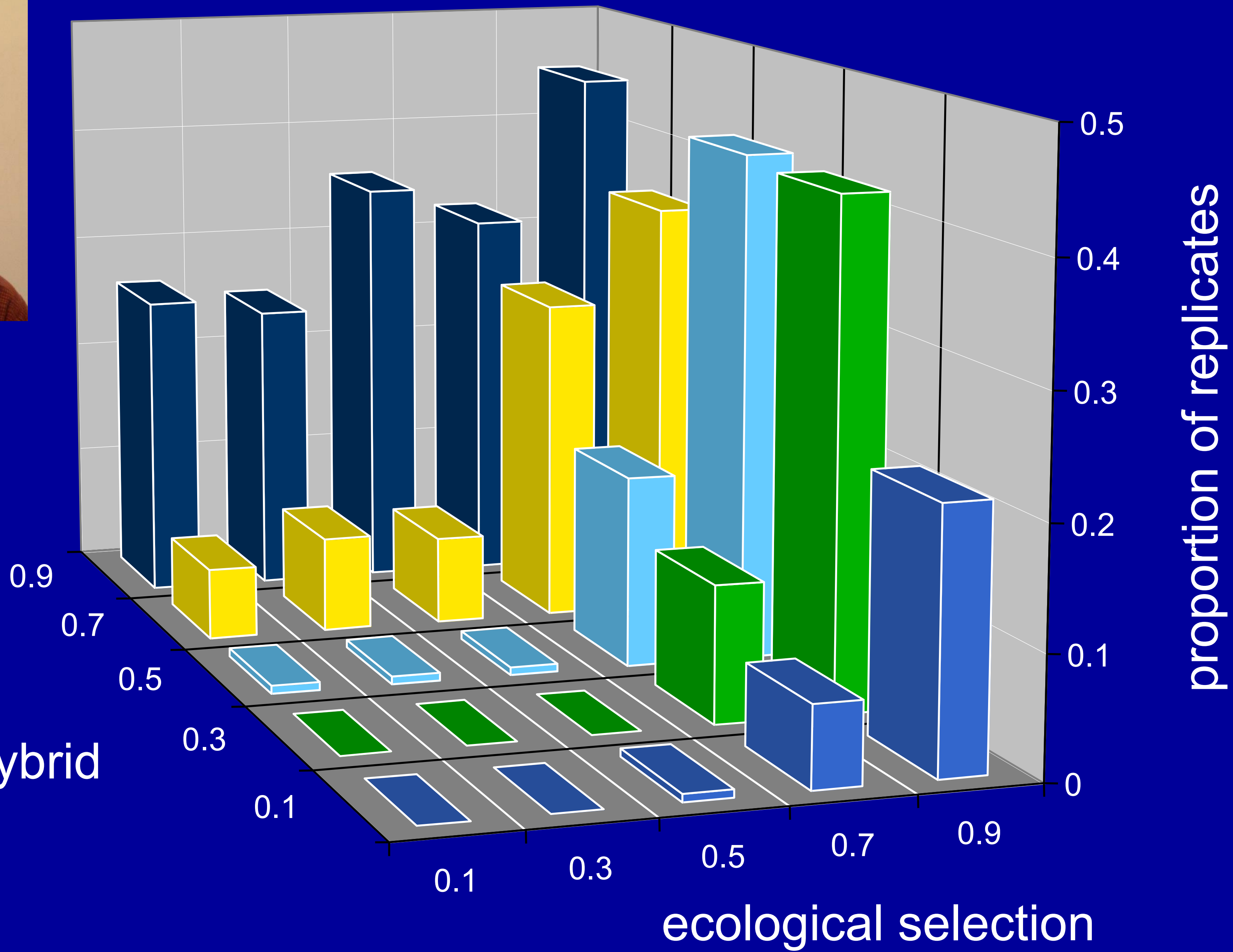
New homokaryotype confers partial isolation with parentals

Genetic incompatibilities model

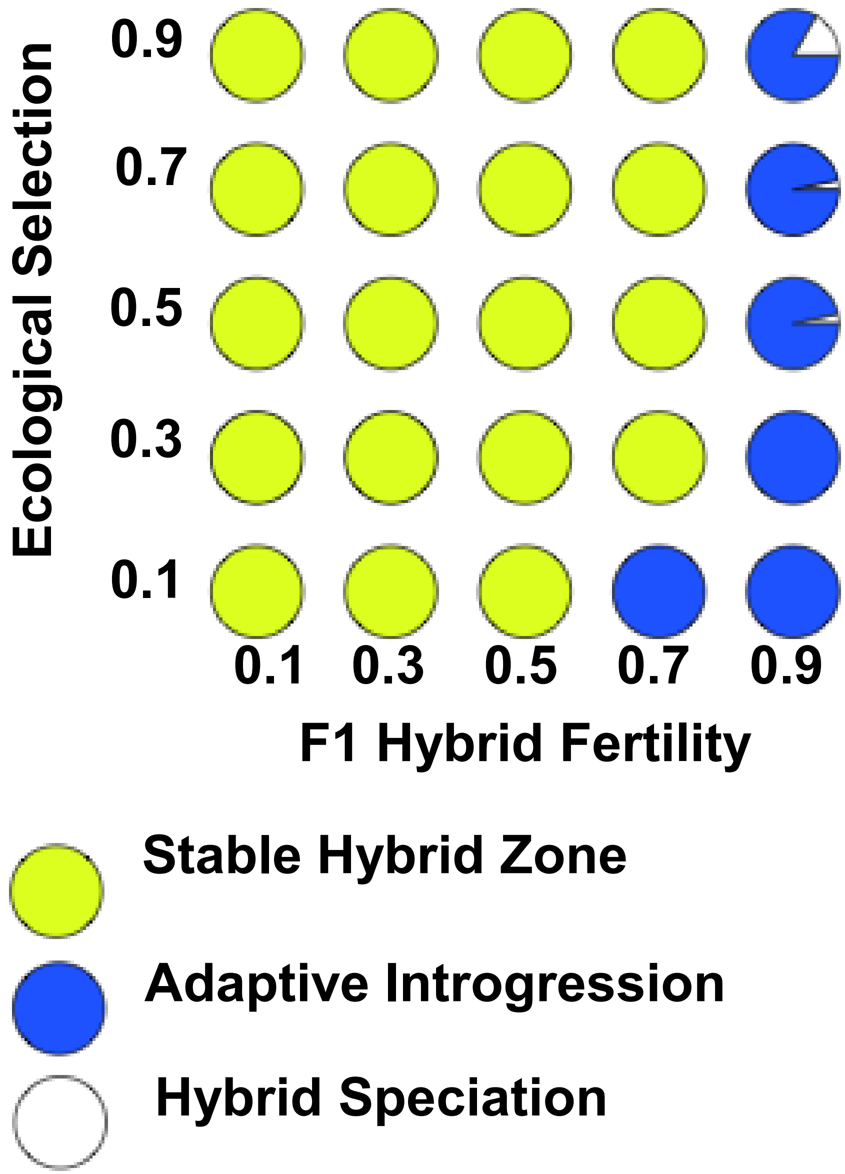


Schumer M, Cui R, Rosenthal GG, Andolfatto P (2015) Reproductive Isolation of Hybrid Populations Driven by Genetic Incompatibilities. PLOS Genetics 11(3): e1005041. https://doi.org/10.1371/journal.pgen.1005041
https://journals.plos.org/plosgenetics/article?id=10.1371/journal.pgen.1005041

Hybrid Speciation Model (open habitat available for hybrids)



Frequency of Hybrid Speciation
(no open habitat available for hybrids)



Buerkle et al. (2003)

CONDITIONS FAVORING HOMOPLOID HYBRID SPECIATION

- **Little spatial isolation between parental species, but substantial isolation of hybrid species.**

- **Open habitat for hybrid species.**

- **Strong ecological selection favoring hybrid lineage in new habitat.**

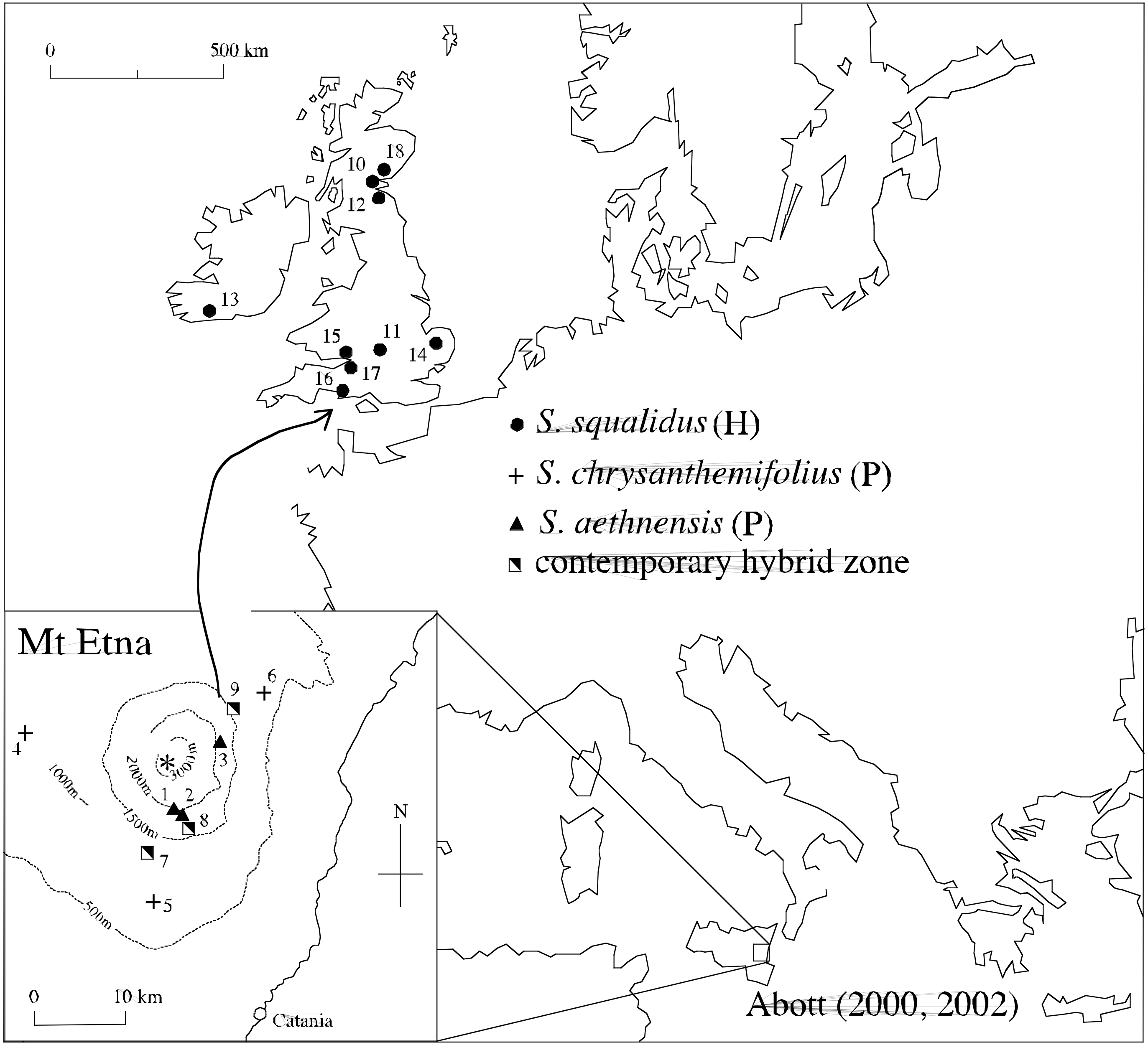
- **Weak postzygotic isolation between parental species, but strong isolation of hybrid species.**

- **Hybrid trait causes assortative mating (not modeled)**


The *Senecio* hybrid zone on Mount Etna, Sicily.
3000m
2000m
1000m
0m
Senecio aethnensis
Hybrid zone
Senecio chrysanthemifolius

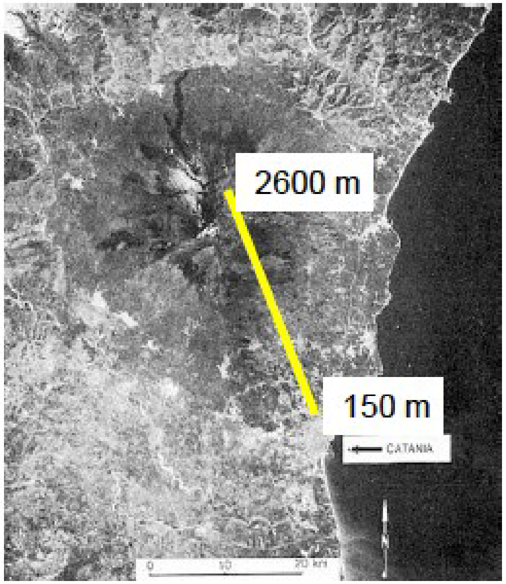
EMPIRICAL EVIDENCE: SPATIAL ISOLATION

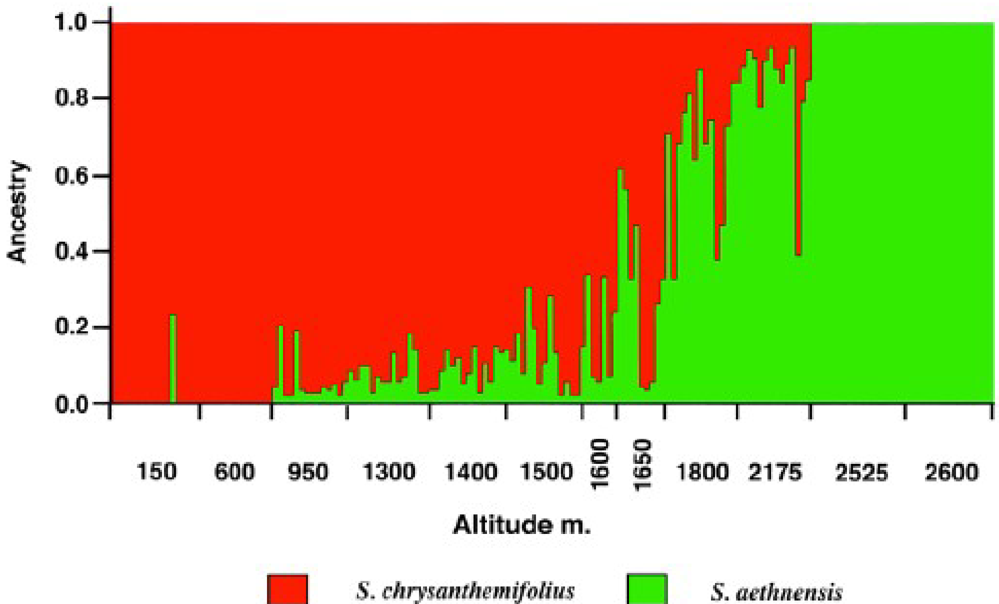
(allopatric origin of oxford ragwort, *Senecio squalidus* (Abbott, 2000, 2002)



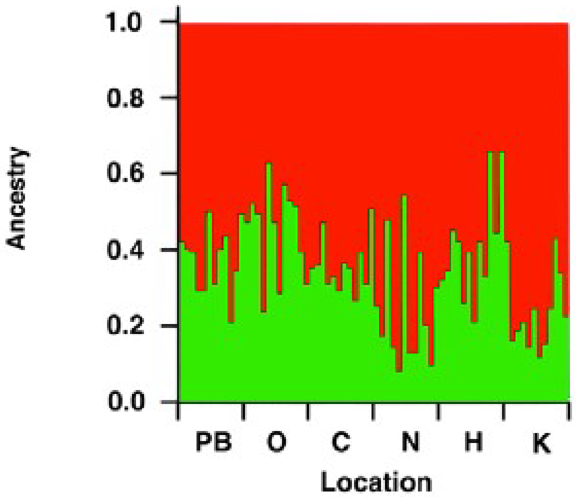
EMPIRICAL EVIDENCE: Admixture
(allopatric origin of oxford ragwort, *Senecio squalidus*)

Ancestry of plants along altitude gradient, Mt Etna



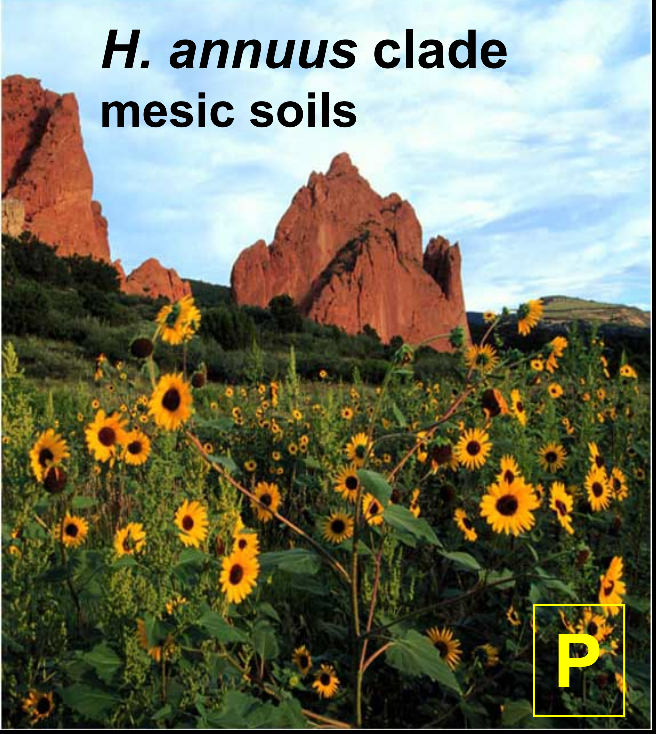


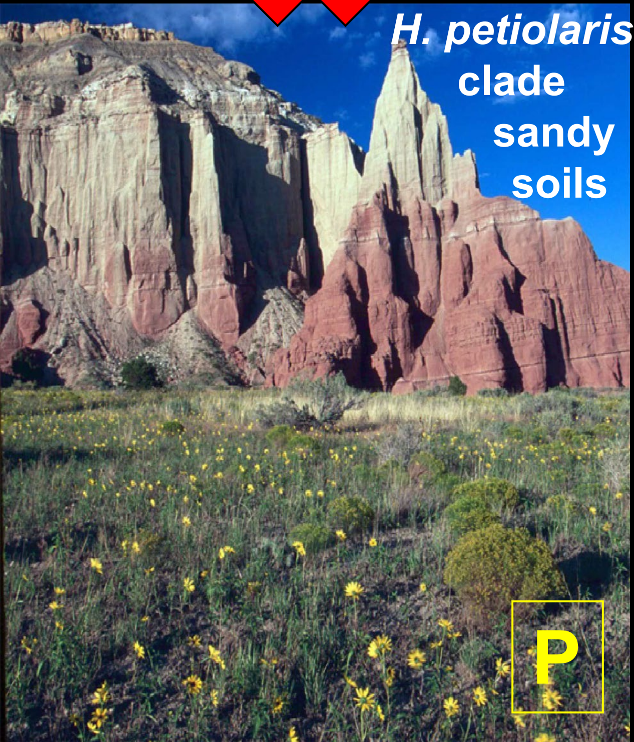
Ancestry of *S. squalidus* plants in UK



James JK, Abbott RJ (2005) Evolution 59: 2533-2547

EMPIRICAL EVIDENCE: ECOLOGICAL ISOLATION





Reciprocal transplant experiments indicate that synthetic and natural hybrids favored in hybrid habitats.

TESTING THE IMPORTANCE OF ECOLOGY IN HYBRID SPECIATION

- **Are the stabilized hybrid species ecologically divergent from their parents?** **YES - for all but one species tested**

- **Are the hybrid species favored in the hybrid habitats?**

  YES - for *Helianthus*

- **Is there evidence of parallel hybrid speciation?**

  YES - for *Argyranthemum, Pinus*

HYBRID TRAITS CAUSE ASSORTATIVE MATING

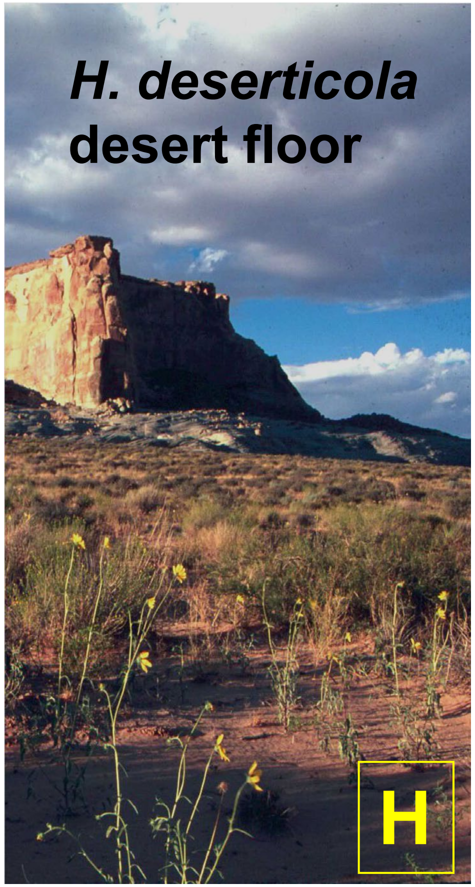
Helianthus deserticola (flowering time)
Rieseberg 1991

Heliconius heurippa (wing pattern)
Maverez et al. 2006

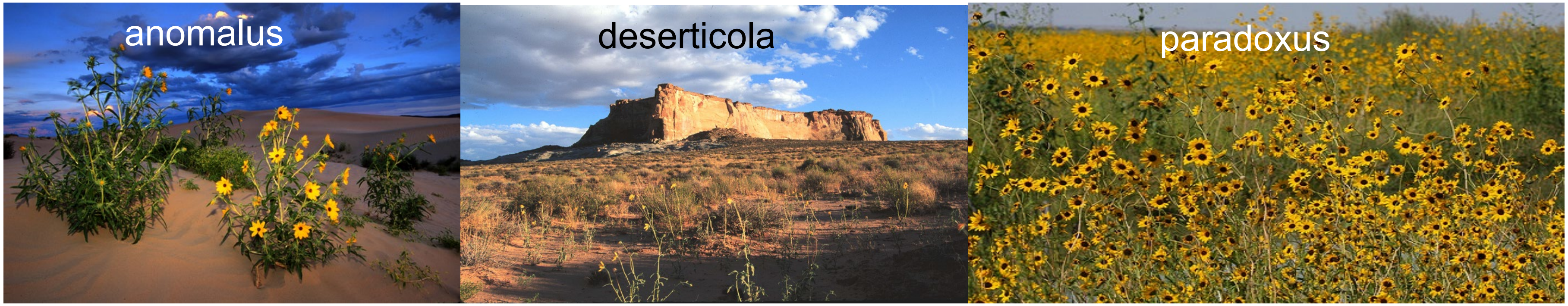
Iris nelsonii (flower color)
Arnold 1993

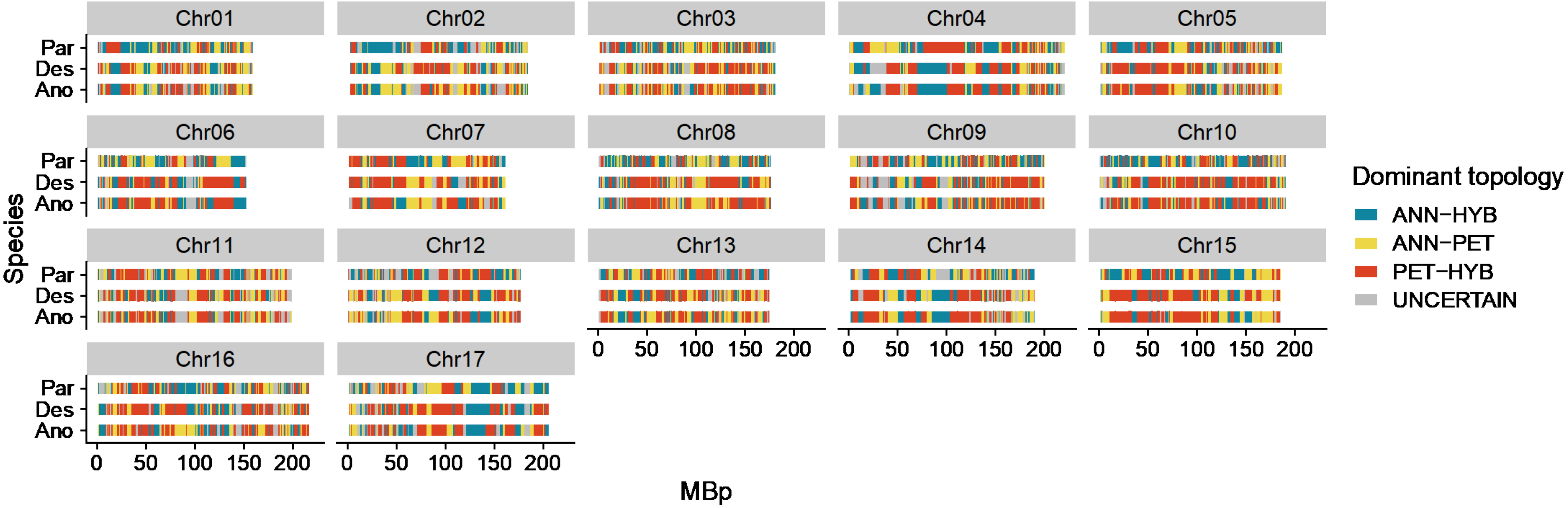
Penstemon clevelandii (flower color)
Wolf et al. 1998

Xiphorus clemenciae (swordtail)
Meyer et al. 2006



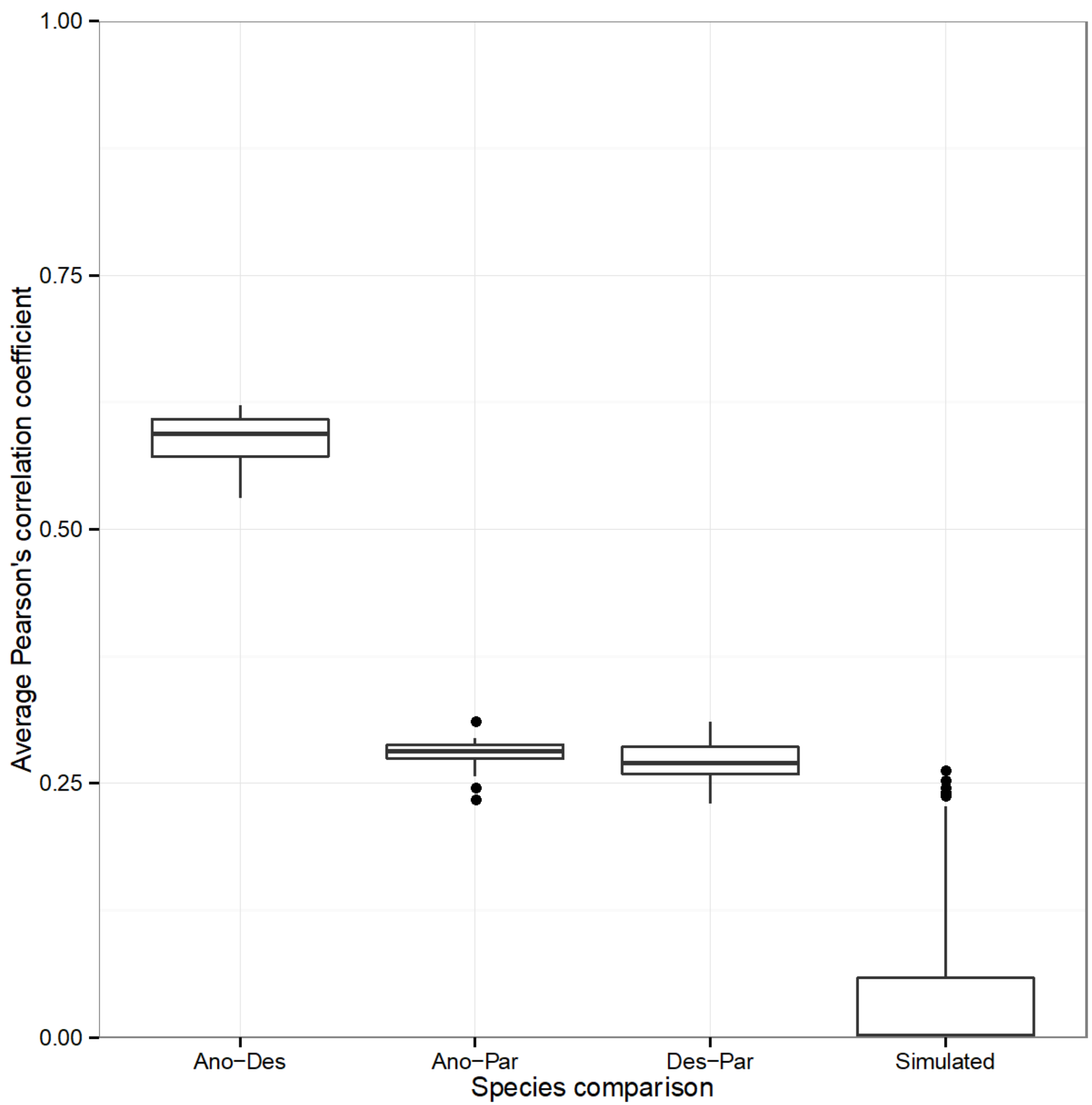
WHAT HAPPENS TO THE GENOME OF HYBRID SPECIES?

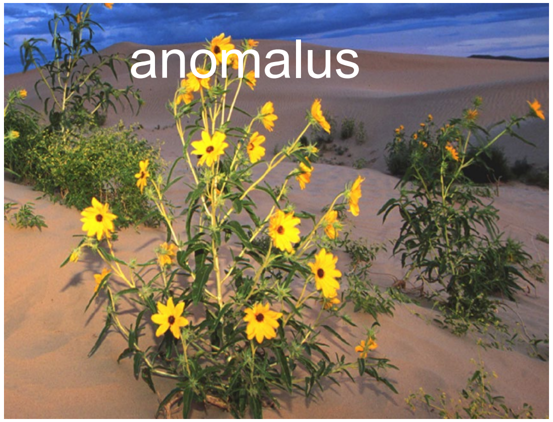




Greg Owens, unpublished

HYBRID SPECIATION IS SURPRISINGLY REPEATABLE AT THE GENOMIC LEVEL





Greg Owens, unpublished

Unanswered Questions

- Is hybridization an important extinction threat?
- Does introgression often contribute to the evolution of invasive species?
- Is reinforcement frequent? Have we been looking at the wrong traits?
- Have most species experienced one or more episodes of hybridization in their evolutionary history (i.e., is strict allopatric speciation rare)?