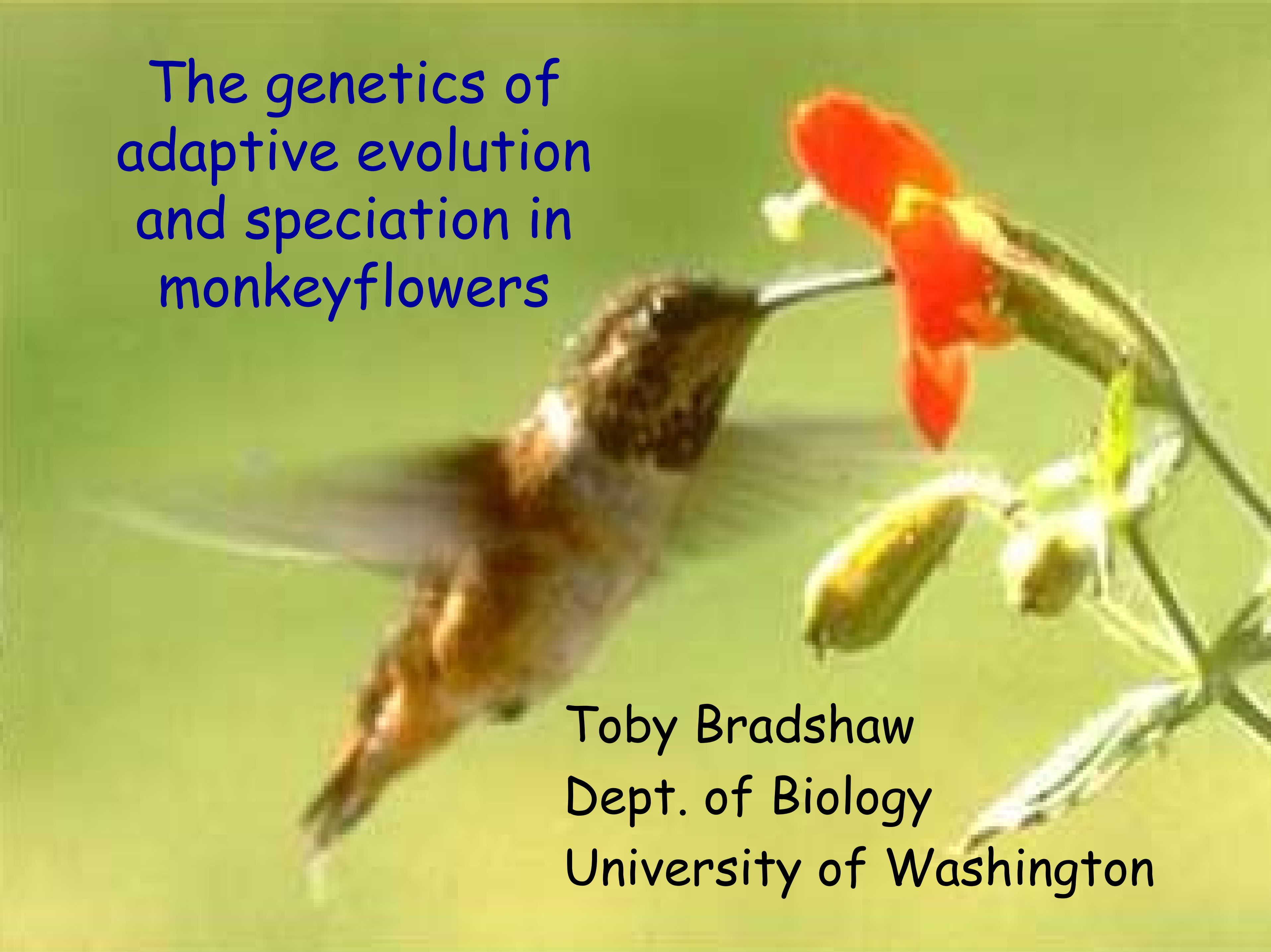
The genetics of adaptive evolution and speciation in monkeyflowers



Toby Bradshaw
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University of Washington

Why are there species?

"… the living world is not a formless mass of randomly combining genes and traits, but a great array of … gene combinations, which are clustered on a large but finite number of adaptive peaks." – Theodosius Dobzhansky

Mimulus

Mimulus as a model for ecological and evolutionary genetics

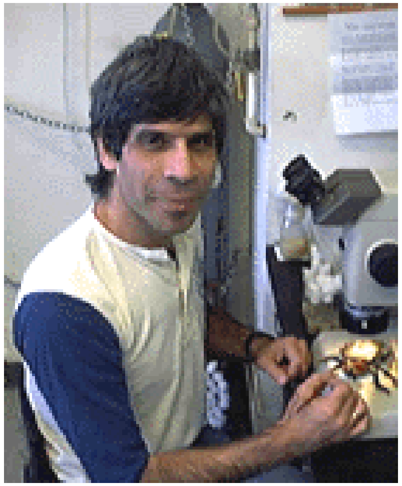
- ~160 species worldwide, with major radiations in western North America and Australia
- well-resolved phylogeny (except for the *M. guttatus* species complex)
- occupy habitats from sea level to alpine, desert to riparian to aquatic
- life history/habit/mating system diversity – annual, perennial, herbaceous, woody shrub, selfing, outcrossing, mixed, obligately asexual
- phenomenal floral diversity associated with pollination syndromes

Speciation

Biological species concept

“Groups of actually or potentially interbreeding populations reproductively isolated from all other such groups.” – Ernst Mayr

“When we understand the origin of reproductive isolation, we understand the origin of species.” – Jerry Coyne



Reproductive isolation

Pre-mating barriers to gene flow

- Geographic
- Ecological
- Phenological
- Behavioral
- Mechanical

Post-mating barriers to gene flow

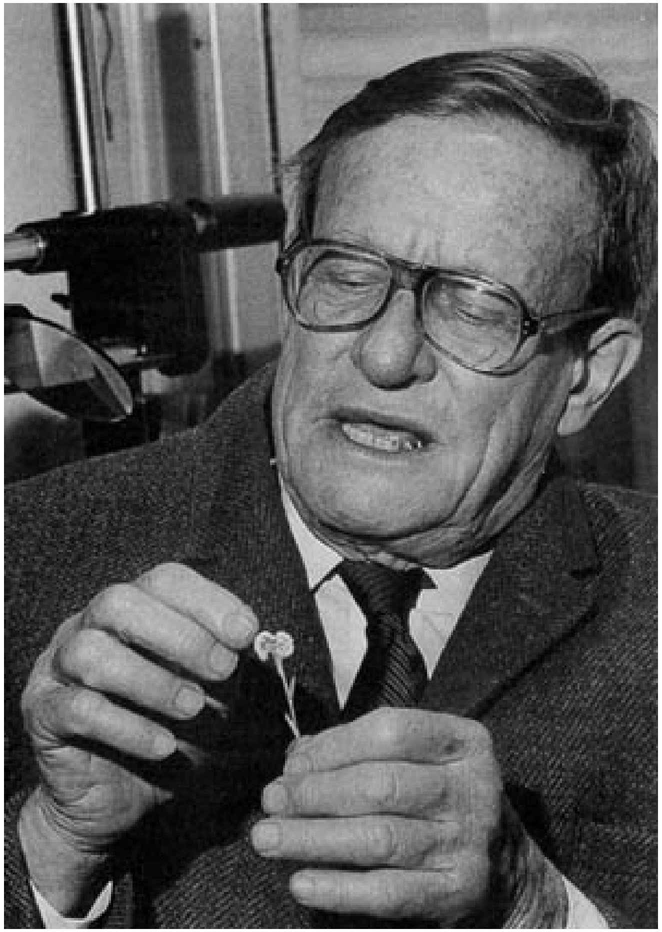
- Gamete incompatibility
- Sperm competition
- Hybrid inviability
- Hybrid sterility
- Hybrid breakdown

Jordan’s law

“Given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort.” -- David Starr Jordan (1905) *Science* 22: 545-562.

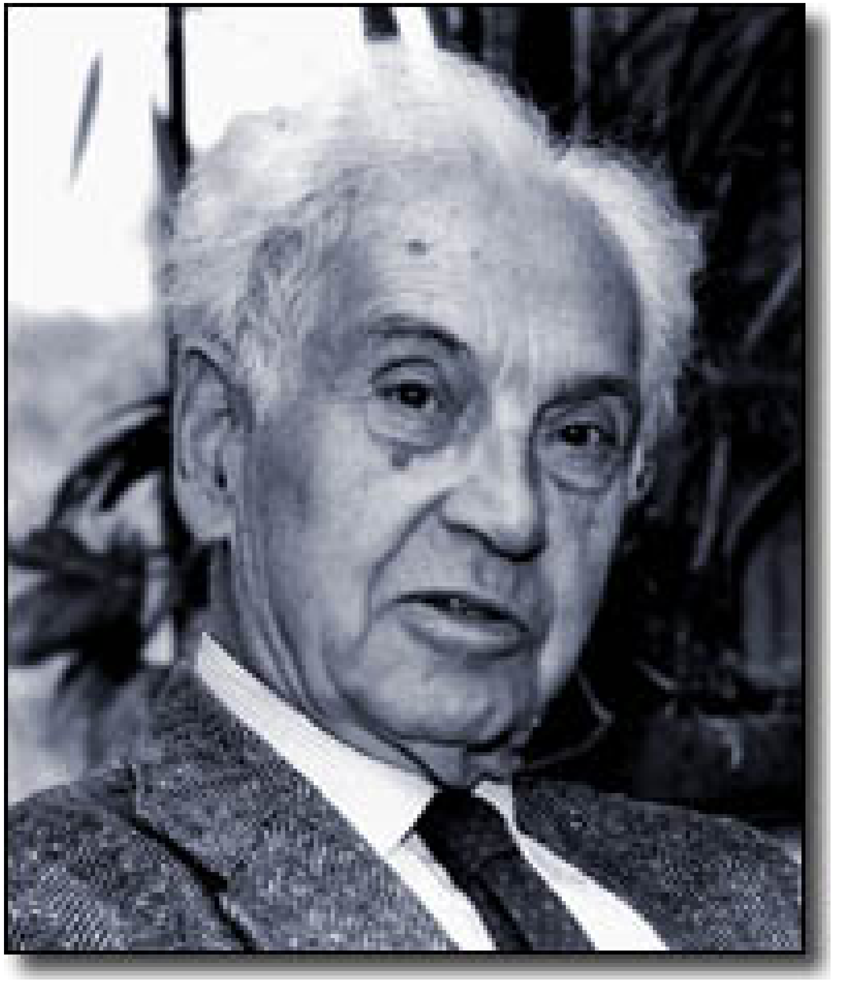
The origin of reproductive isolation by ecogeography

"By far the commonest type of isolation in both the plant and the animal kingdom is that resulting from the existence of related types in different geographical regions which differ in climatic and edaphic conditions." – G. Ledyard Stebbins (1950) *Variation and Evolution in Plants*

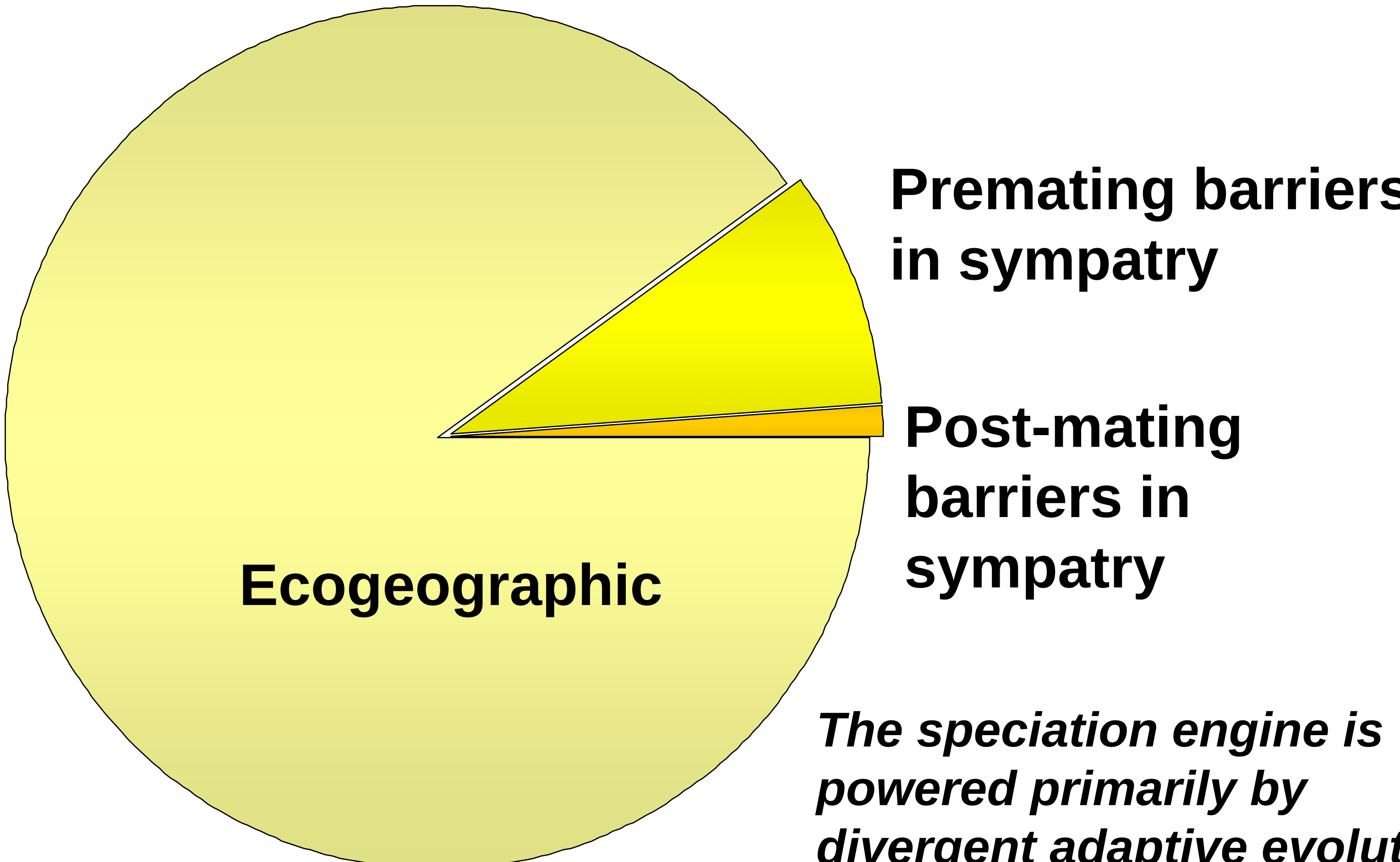


The origin of reproductive isolation by ecogeography

"... not a single geographic race is known that is not also an ecological race; nor is there an ecological race that is not at the same time at least a microgeographic race."
-- Ernst Mayr (1963)
Animal Species and Evolution



The Jordan/Stebbins/Mayr pie diagram for mechanisms producing reproductive isolation



The speciation engine is powered primarily by divergent adaptive evolution

Why use non-model plant systems?

Good genomics is faster than good ecology

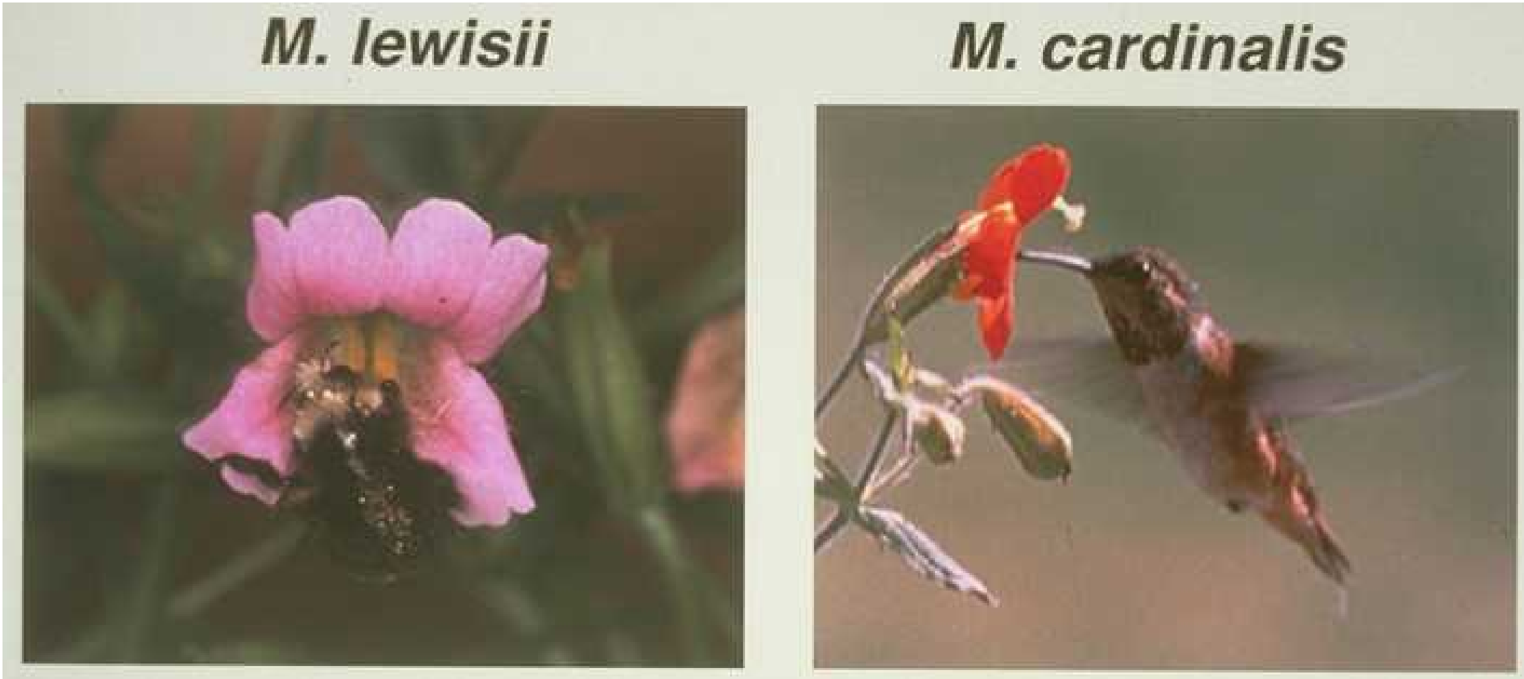
- The whole *Mimulus* genome can be sequenced in less than one greenhouse generation, and in about 10% the length of a field season.

Genetic model systems are usually chosen for the same reasons that ecologists avoid them

- Small size, adapted as human commensals or to human-disturbed habitats

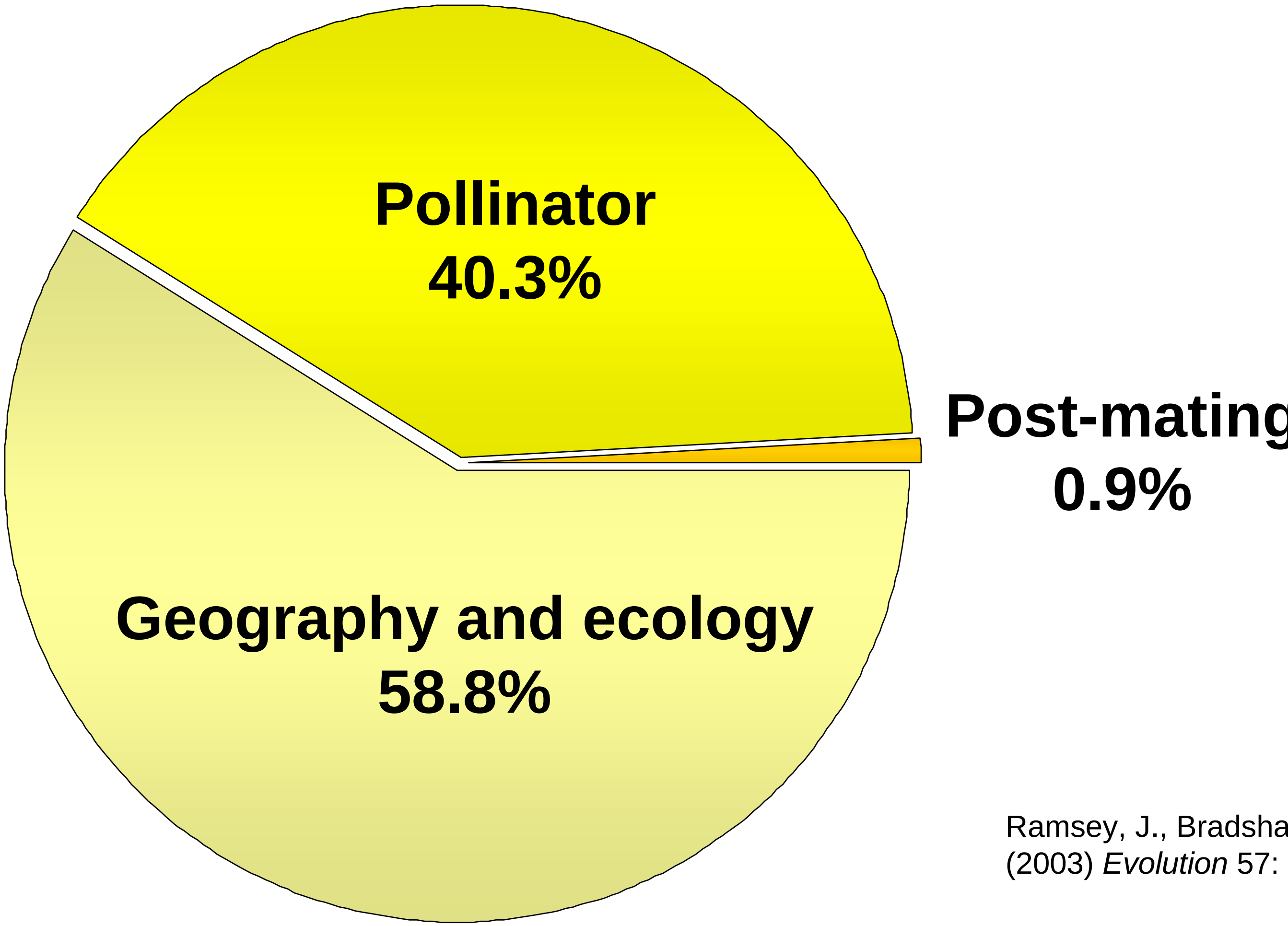
Mimulus as a model for ecological and evolutionary genetics

>70 years of work on ecology, evolution, and genetics, starting with Clausen, Keck, and Hiesey in 1929



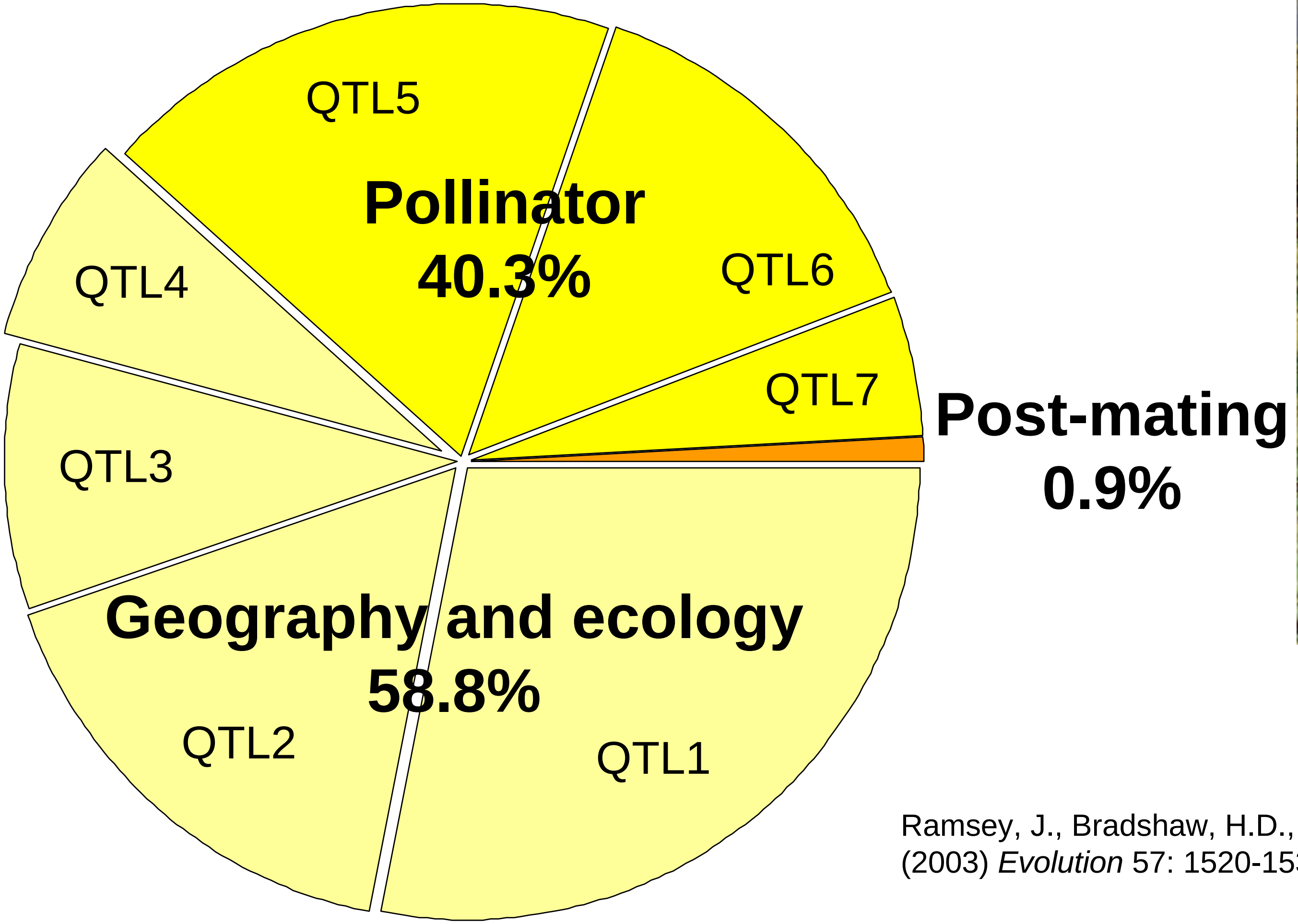
Bumblebee-pollinated	Hummingbird-pollinated
Pink	Red
Wide corolla opening	Narrow, tubular corolla
Inserted stigma/anther	Exserted stigma/anther
1-2μl nectar	40-100μl nectar
Mid-high elevation	Low-mid elevation

Components of reproductive isolation between *M. lewisii* and *M. cardinalis*



Ramsey, J., Bradshaw, H.D., Jr., & Schemske, D.W. (2003) *Evolution* 57: 1520-1534.

Components of reproductive isolation between *M. lewisii* and *M. cardinalis*



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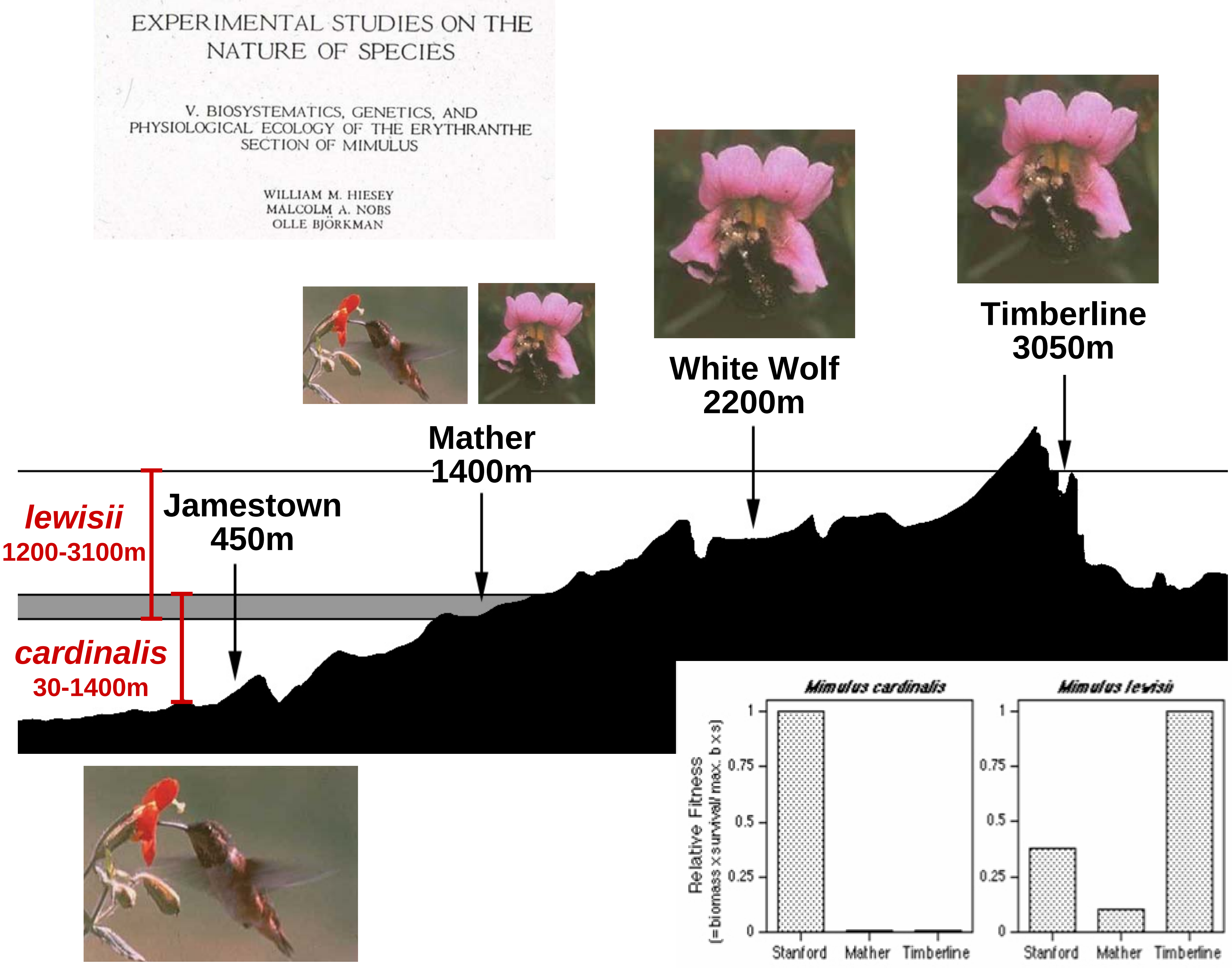
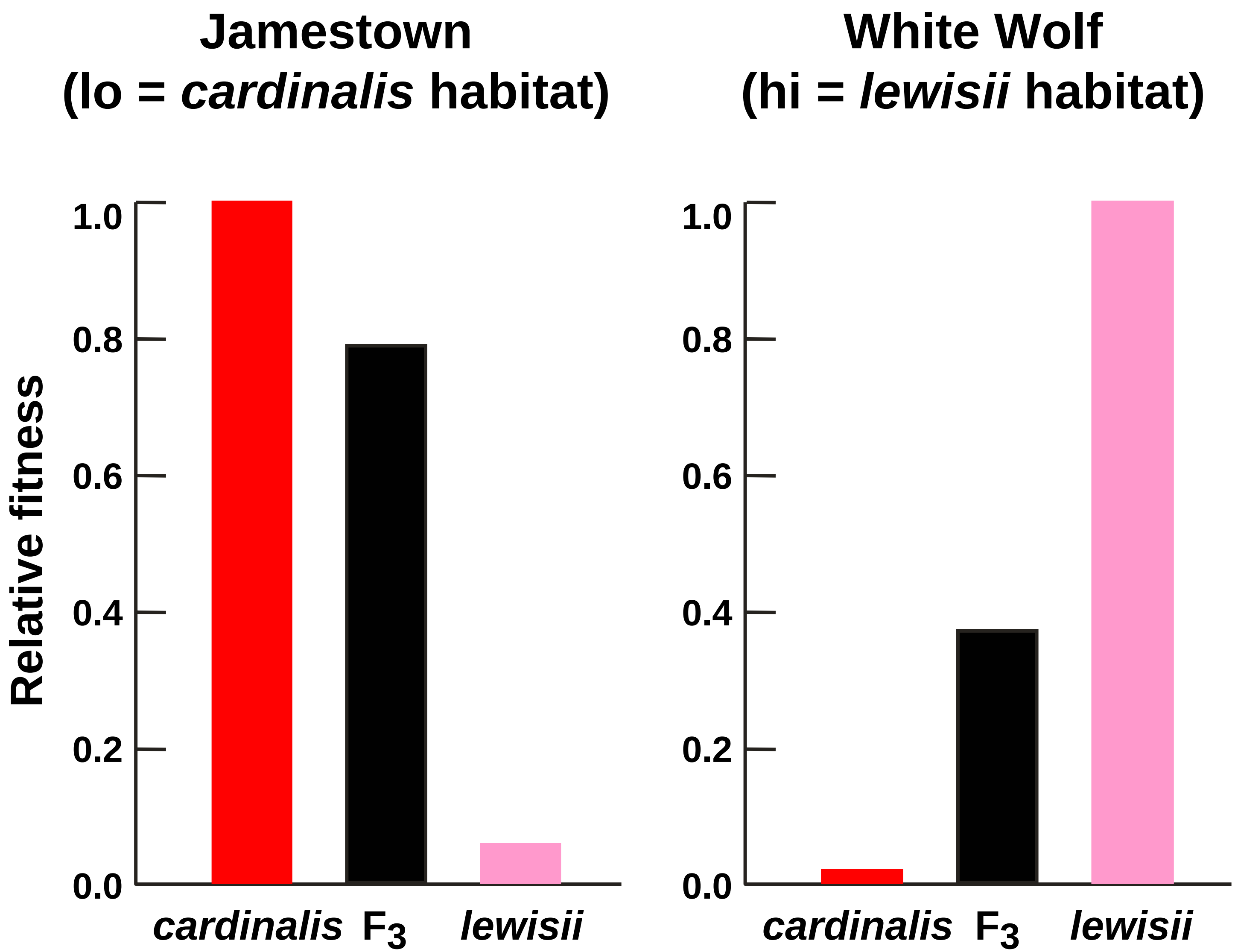

EXPERIMENTAL STUDIES ON THE NATURE OF SPECIES
V. BIOSYSTEMATICS, GENETICS, AND PHYSIOLOGICAL ECOLOGY OF THE ERYTHRANTHE SECTION OF MIMULUS
WILLIAM M. HIESEY
MALCOLM A. NOBS
OLLE BJÖRKMAN
Timberline
3050m
White Wolf
2200m
Mather
1400m
Jamestown
450m
lewisii
1200-3100m
cardinalis
30-1400m
Mimulus cardinalis
Mimulus lewisii
Relative Fitness
(=biomass x survival/ max. b x s)
1
0.75
0.5
0.25
0
Stanford
Mather
Timberline

Relative Fitness of Parents and F1 Hybrids



Experimental evolution in nature: the “Δp” Experiment

M. cardinalis
30m-1400m

X

M. lewisii
1200m-3100m

F_1

↓

F_2

↓

F_3

field transplant
N = 4,755 seedlings

field transplant
N = 8,032 seedlings

low elevation
(Jamestown,
450m)

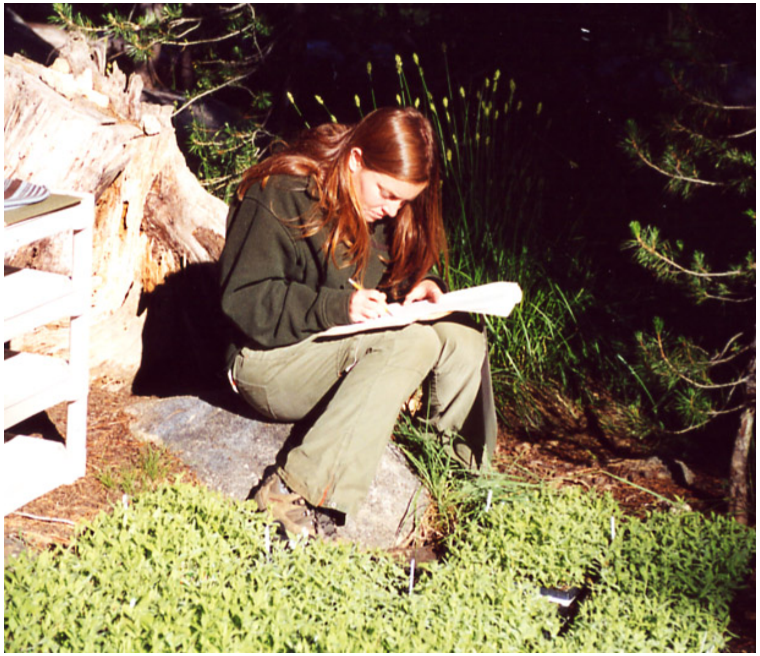
greenhouse
N = 500
seedlings

high elevation
(White Wolf,
2200m)

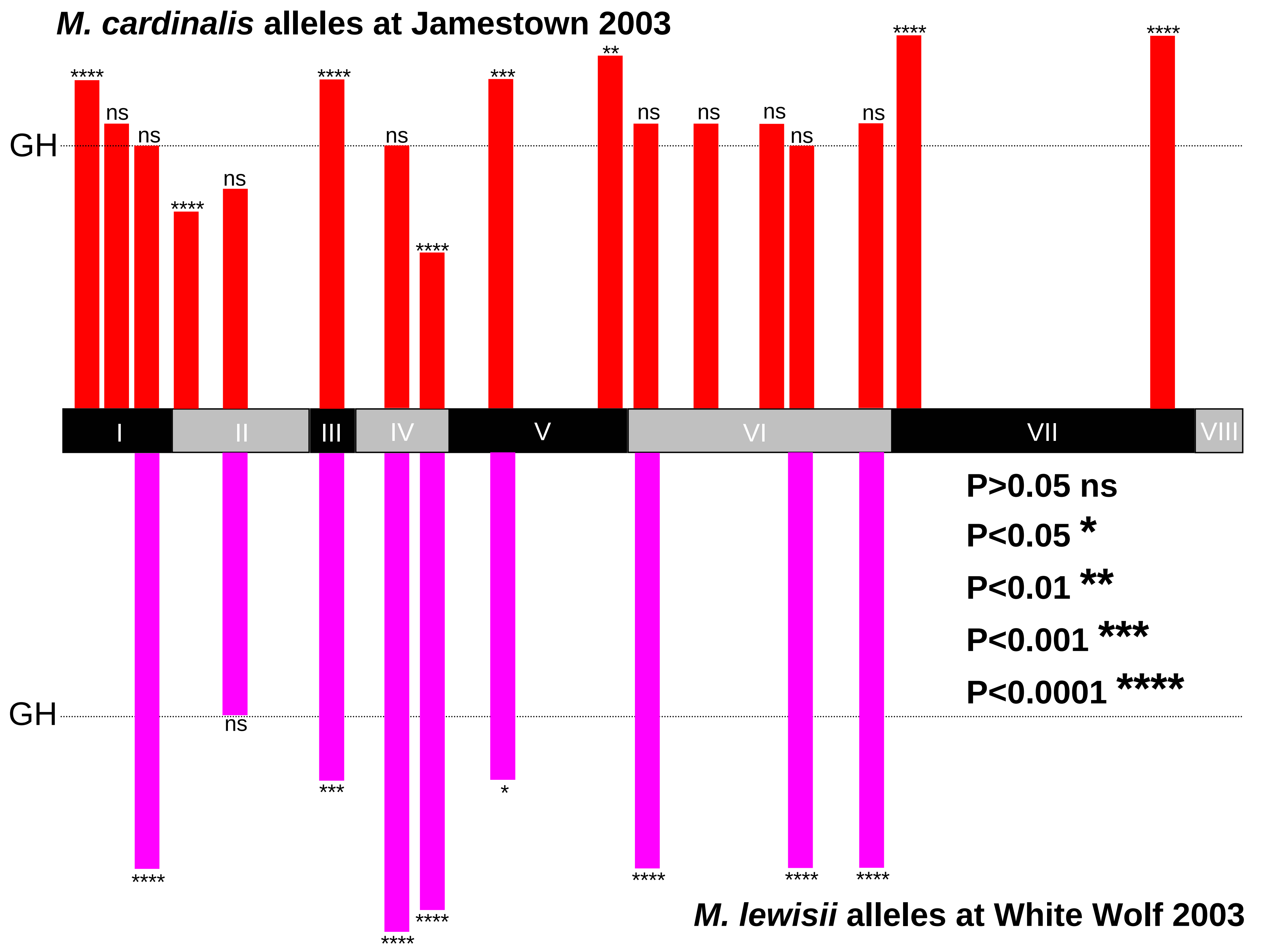
fates: dead | survive to flower | survive to flower | survive to flower | dead

genotype random sample with genome-wide markers: low elevation survivors | greenhouse survivors | high elevation survivors

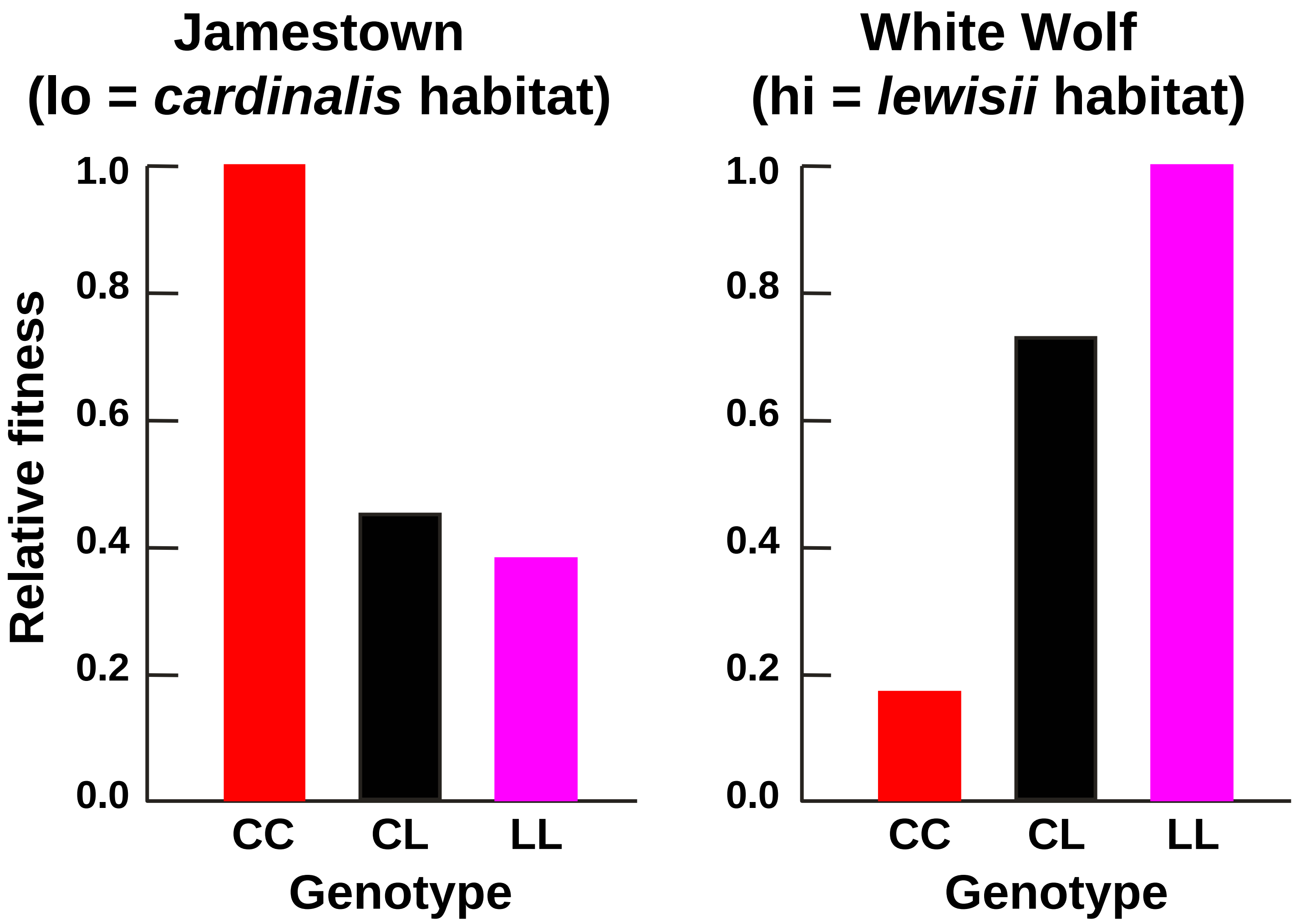
calculate the change in allele frequency at each locus across the genome: Δp low elevation | Δp high elevation




Hard Rock


M. cardinalis alleles at Jamestown 2003
GH
GH
****
ns
ns
****
ns
****
ns
****
***
**
ns
ns
ns
ns
ns
****
****
I
II
III
IV
V
VI
VII
VIII
****
ns
***
****
****
*
****
****
****
P>0.05 ns
P<0.05 *
P<0.01 **
P<0.001 ***
P<0.0001 ****
M. lewisii alleles at White Wolf 2003

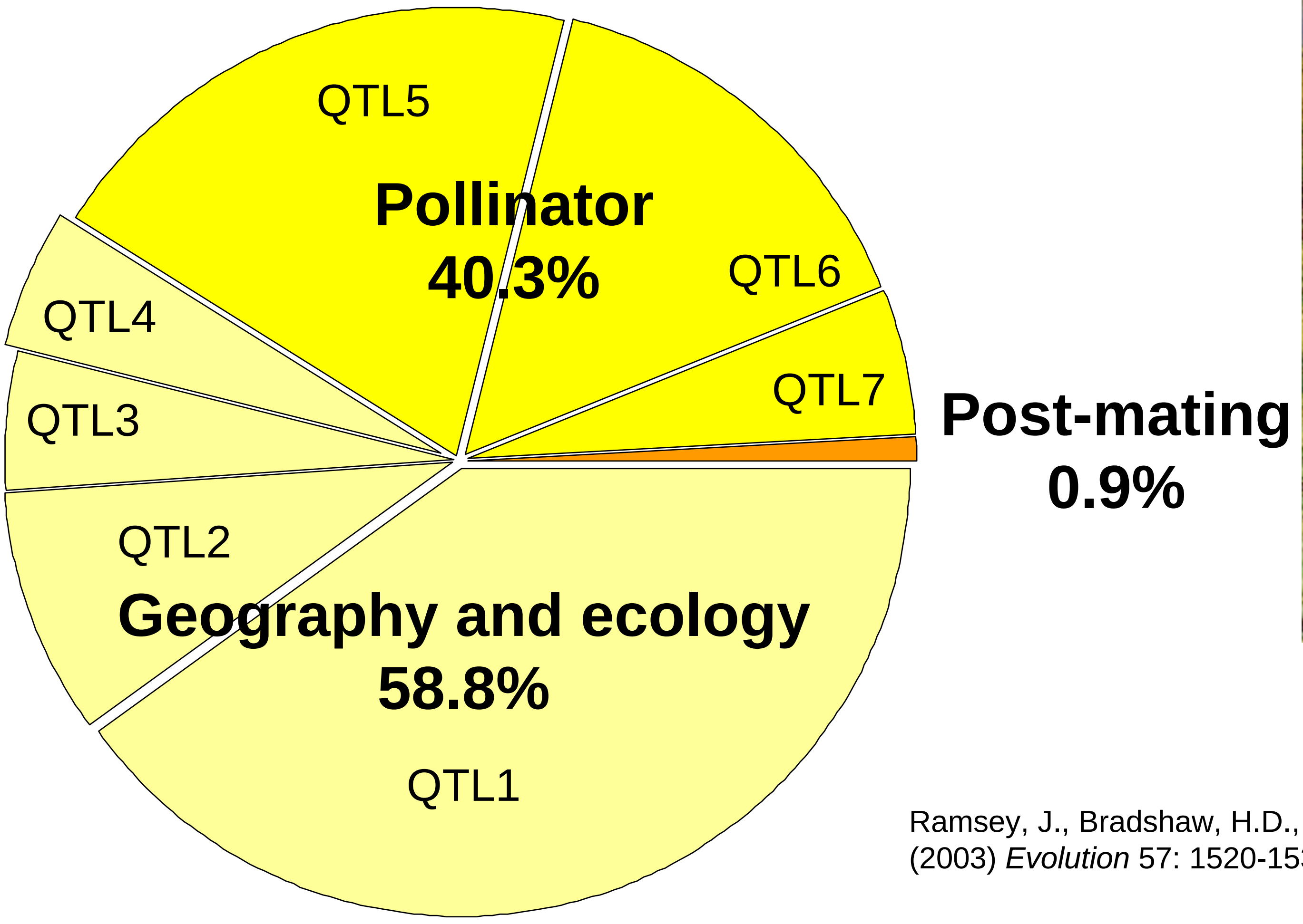
Relative fitness of F_3 genotypes at MgSTS46 (LG III)



Conclusions

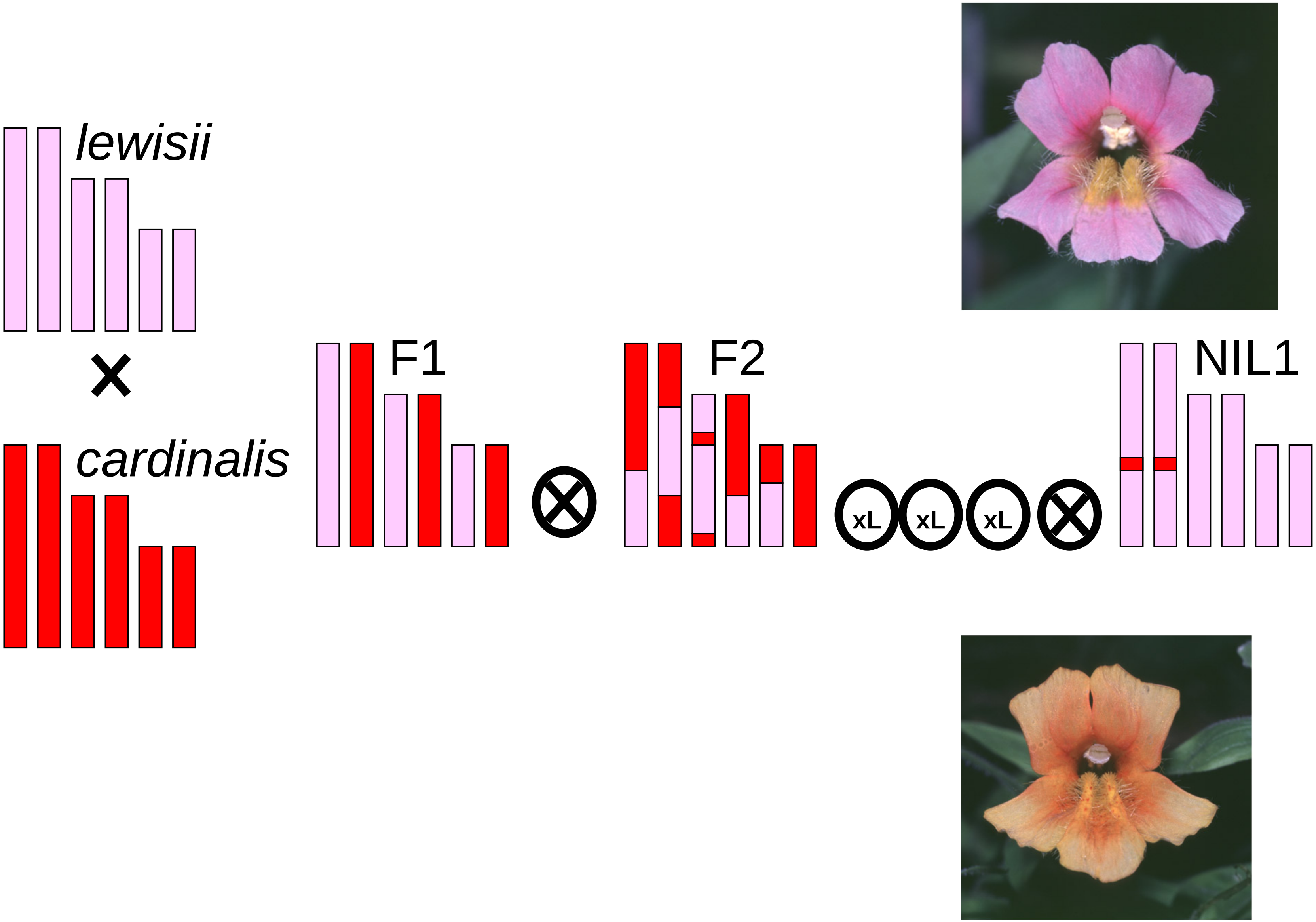
- Differential adaptation is responsible for most of the reproductive isolation between *M. lewisii* and *M. cardinalis* (and, according to Jordan's law, most other pairs of sister taxa).
- QTLs distributed throughout the genome affect local adaptation, with some showing fitness tradeoffs between environments.

Components of reproductive isolation between *M. lewisii* and *M. cardinalis*



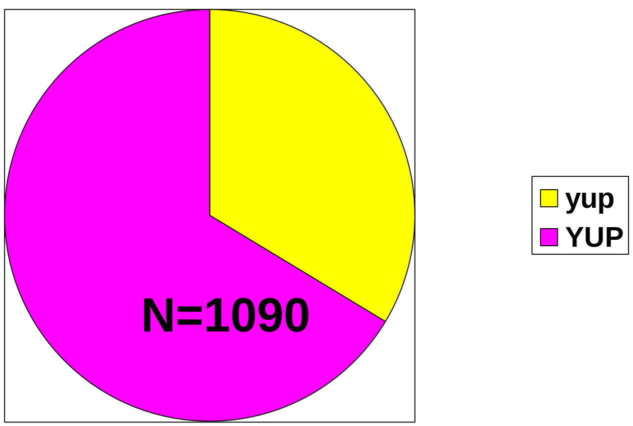
Ramsey, J., Bradshaw, H.D., Jr., & Schemske, D.W. (2003) *Evolution* 57: 1520-1534.

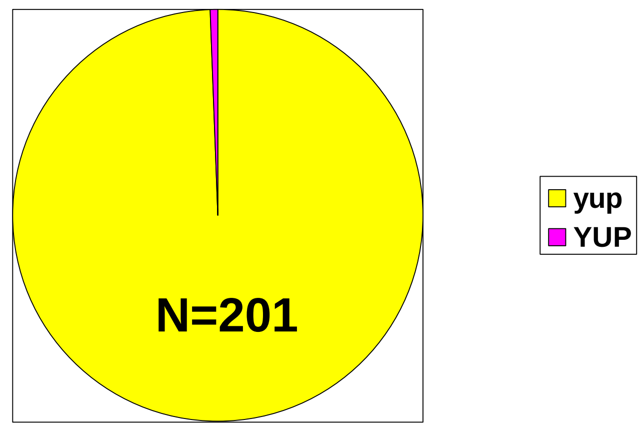
Near-isogenic lines (NILs)




Budget
Truck Rental
Grumman


CAPPY'S
367-0151
SEATTLE, WA
5726-003
196
Road Runner

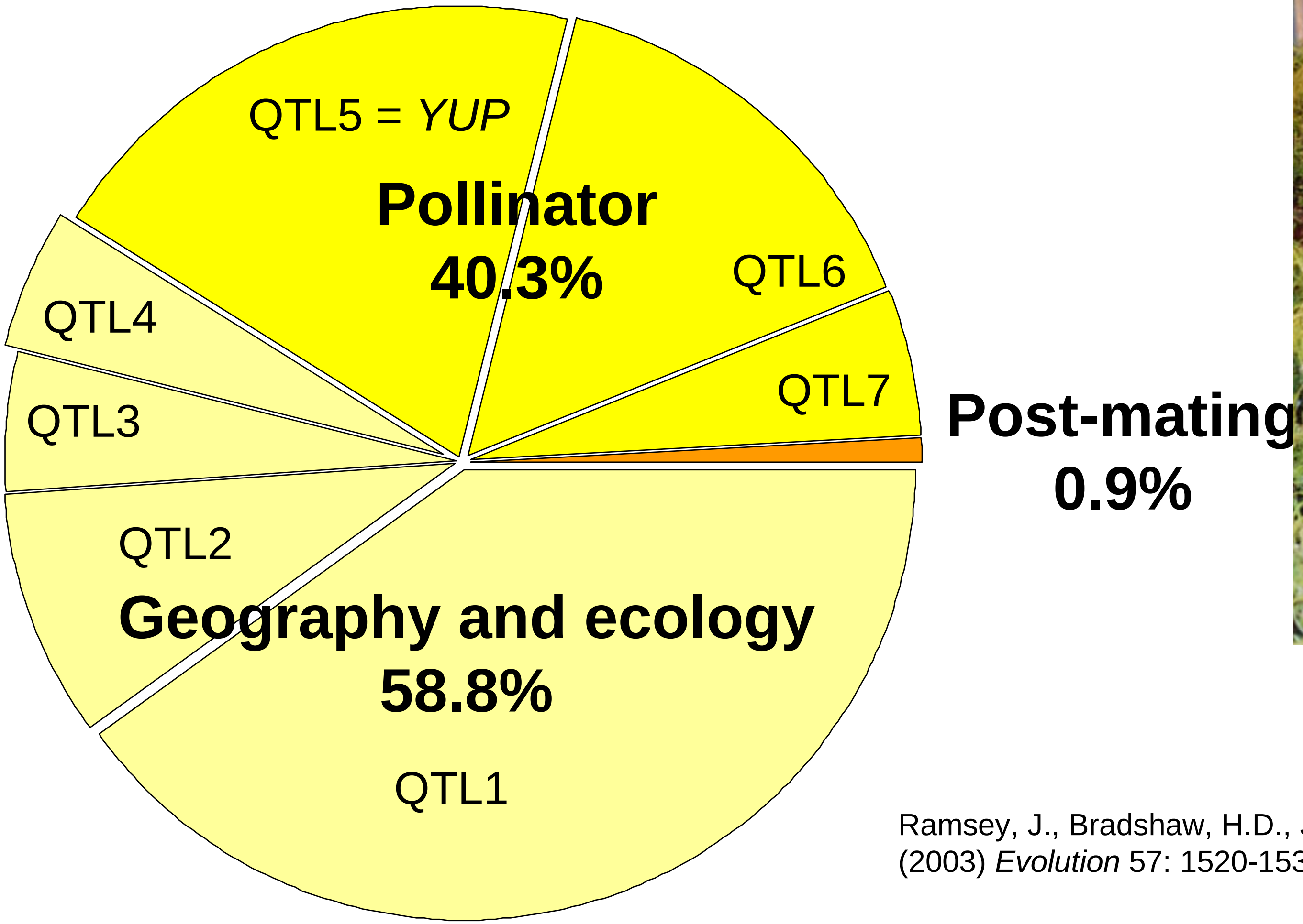




Bumblebees **Hummingbirds**

Bradshaw & Schemske (2003) *Nature* 426: 176-178.

Components of reproductive isolation between *M. lewisii* and *M. cardinalis*



Ramsey, J., Bradshaw, H.D., Jr., & Schemske, D.W. (2003) *Evolution* 57: 1520-1534.

Conclusions

Major QTLs control all aspects of reproductive isolation in *Mimulus*, from ecogeographic (allopatric) to pollinator preference (sympatric).

The tempo of speciation depends on the genetic details – are these major QTLs single genes, or clusters of linked genes?

From QTLs to genes?

For the traits producing the greatest reproductive isolation in allopatry (**adaptation to elevation**) and sympatry (**carotenoid pigment deposition**) there are no obvious candidate genes. Until there are ...

Two options:

- Positional cloning of major QTLs
- Mutagenesis (at least when one QTL allele is recessive)

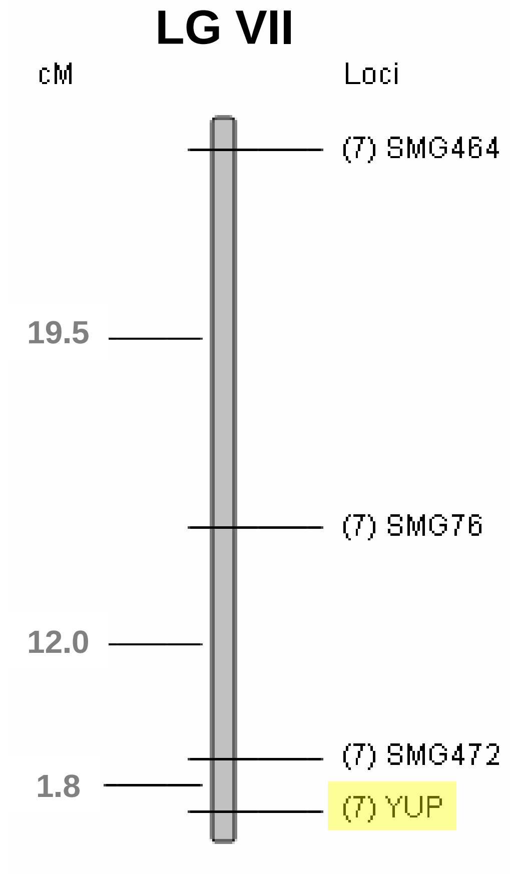
Mimulus as a model for ecological and evolutionary genomics

- NSF FIBR project (2004-2009)
- develop genomics tools and apply them to cloning genes involved in speciation
- attract investigators from “traditional” genetic model systems
- recombinant inbred lines (RILs) for mapping
- near-isogenic lines (NILs) for major QTLs
- sub-cM genetic maps based on EST-derived markers
- physical maps from BAC libraries (2006)
- *Mimulus guttatus* genome sequence from JGI in 2007!
- transgenesis
- mutagenesis

LIGHT AREAS

plus:
FLOWERING TIME1
PISTIL LENGTH1
~100 new markers from JGI

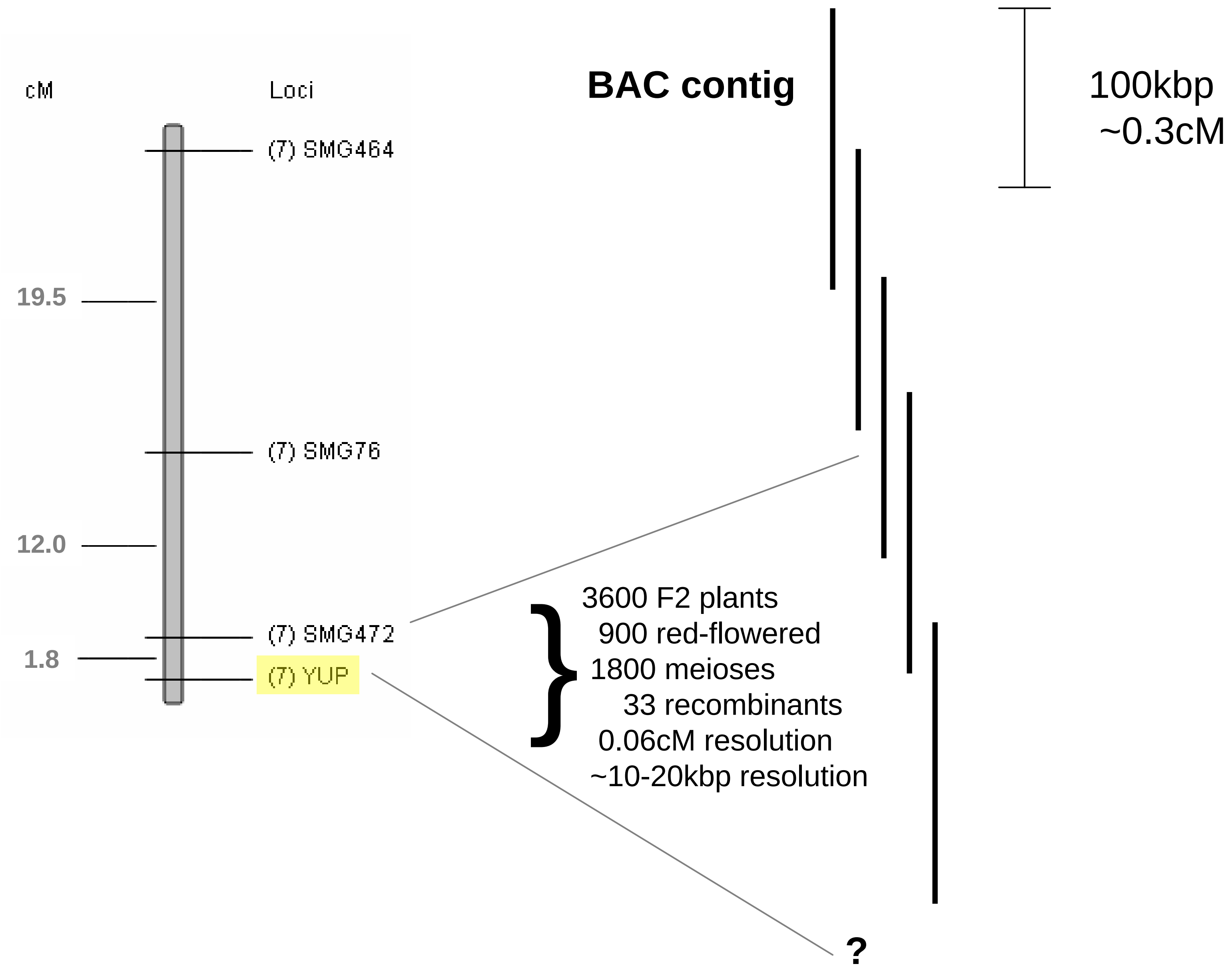
wt *M. lewisii*



ROSE INTENSITY

REFLEX1

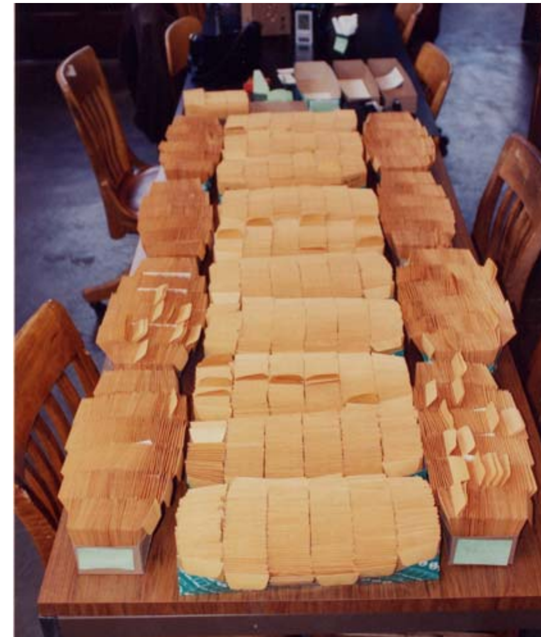
YELLOW UPPER



cM
Loci
BAC contig
100kbp
~0.3cM
(7) SMG464
19.5
(7) SMG76
12.0
(7) SMG472
1.8
(7) YUP
3600 F2 plants
900 red-flowered
1800 meioses
33 recombinants
0.06cM resolution
~10-20kbp resolution
?

EMS mutagenesis of *M. lewisii*

- Christina Pince
- 1776 M1 lines
- 31,968 M2 plants



M. lewisii mutants

M. bifidus

M. parishii

M. inconspicuus

wt *M. lewisii*

M. douglasii

M. cardinalis

Conclusions

Many phenotypes that characterize the radiation of floral form across the genus *Mimulus* seem to be controlled by single loci

There is an opportunity to describe a large-scale adaptive radiation at the level of individual genes

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